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7.—Natural distribution and speciation of marine animals

Presidential Address, 1968

by R. W. George*

Delivered 15 July, 1968

Introduction

Descriptive analyses of the distribution of marine animals have been given by many workers, the broadest approach being that of Ekman (1953). He brought together separate analyses by other workers to produce the first world-wide synthesis of animal distribution in the sea in his book entitled, "Zoogeography of the sea". Since that time his definition and terminology of marine zonation both horizontal and vertical have been virtually unchallenged and the book remains one of today's major references.

But Ekman's book was purely descriptive and gave little indication of the mechanisms which originally produced and then maintained the zones as relatively discrete units. His explanation for the separate tropical shallow water faunas are clear enough where physical land bridges exist, i.e. the Panama and South-West Asian land bridges; but "oceanic barriers", although undisputed for many species, receive a circular explanation. He defines the fauna he is comparing as shallow water, tropical stenothermal species with short-lived larvae and, by definition, it follows that passive or active migration across or around the "East Pacific Barrier" or the "Mid-Atlantic Barrier" are impossible for the animals with those attributes.

But what happens if species do have long-lived larvae? One would expect satisfactory occupation in another faunal zone, if the ability to cover large distances were the only necessity to conquer the barrier. The spiny lobster *P. penicillatus*, because of its long pelagic larval life, is able to cross the East Pacific Barrier, but it does not "compete" with the East Pacific mainland species of spiny lobster at all, living only on the offshore islands, e.g. Galapagos, Clipperton, Cocos (Holthuis & Loesch 1967). This species of spiny lobster (and the "Transpacific" fish of Briggs 1961) are "barrier breakers" but do not form part of the fauna on the other side of the barrier. I submit that each species of the fauna on the "other side" is living in environmental conditions to which each has evolved by natural selection and which are incompatible to

the "barrier breaking" species. Ekman also mentions the importance of the marine climate to faunas but only in a negative manner of "climatic deterioration". I suggest that climate acts positively in the shaping of faunas by direct and continual selection of each species at all growth stages from egg to adult.

As is already evident, I will draw on spiny lobsters (Palinuridae) for the examples in this address on natural distribution and speciation in the sea. Some of the assumptions I have made are as follows:

1. The principles of speciation (and all biological activity) apply equally as well to marine as to the terrestrial situation.
2. Coexistence of phylogenetically similar species necessitates the existence of separate sets of environmental parameters (habitats). (Scientists must consciously break from their airconditioned houses, laboratories and cars to define those habitats for each species studied).
3. Climatic conditions (of sea and land) determine the spatial distribution of animals; changes in the distribution pattern of these climatic zones in the world result in similar changes in the geographic distribution of animals.
4. All members of each species throughout their lives are continually influenced by the climatic events of nature, and survival or extinction of species result from its ability to find and inhabit suitable environmental situations (natural selection).

The following questions are very important in the study of marine speciation:

- What are the earth's basic biological factors?
- What is the marine environment?
- What are ways in which the marine environment can change with time?
- What are the environmental parameters of paramount importance to the species selected for study?
- What have been the effects of past environmental changes in the evolution of the species studied?

*Western Australian Museum, Perth.

The earth's basic biological factors

The basic attributes of this planet are naturally of major significance to every animal (and plant) living on earth: These are:

Solar radiation—this is the energy source.

Water—this acts as a solvent for all biochemical processes.

Dissolved gases—oxygen and carbon dioxide are the gases most important biologically.

Dissolved chemicals—these are the salts and trace elements taken up by animals in solution from the earth.

At any given location on earth the supply of these factors is comparatively constant since direct solar radiation is a function of latitude and the regional distribution of gases and chemicals depends on the distribution of water (rain for terrestrial animals and oceanic circulation for marine animals). The combination of the amounts of all these basic factors in any region of the earth determines the natural environment of that region. In each different environment animals become isolated since each is selected by nature for the particular different combination of environmental factors.

But because of the unequal distribution of heat on the earth's surface, the major earth's media (air and sea) are constantly on the move. Wind belts and ocean currents disturb the animal's environment (described above in static terms). And the animals have evolved particular biological attributes of morphology, behaviour and physiology which are geared to the changes of the environment. Fortunately for the animals, changes in the environment are fairly predictable and it is only when very unusual seasonal events occur that whole communities are wiped out.

This regularity of change of the basic environments is more usually described for terrestrial animals as "the climate" and throughout the world climatic zones and regions are recognised not only by the meteorologists but by the animals too. Scientists who study and recognize these "animal zones" are termed zoogeographers.

In the sea, however, the equivalent of the terrestrial environmental factors of wind, pressure, temperature which make up the climate are not fully reconciled and so no one has been able to forecast the weather under the surface of the sea like they can above it. What is worse is that after an obvious marine meteorological event has occurred, few workers can give reasons for its happening. Bjerknes (1966) has presented a very nice correlation of water circulation abnormalities and abnormalities of the weather patterns over land and sea but how these effects were produced is not known.

The marine environment

The total marine environment is as diverse as we find on the land and is certainly not a uniform and unchanging large volume of salty water. The animals living in it have evolved to meet the many different environmental situations of the sea and have become isolated in some cases by the same sort of physical barriers that we observe on land. In Figure 1a, a diagrammatic section of the land and sea illus-

trates some of these isolated situations. The isolation provided by mountain tops, alpine lakes, mountain slopes, coastal plains and coastal lakes are mirrored, below the sea in the figure, as abyssal trenches, slope basins, continental slopes, continental shelves and continental basins. This analogy is applicable to the bottom living marine animals where physical features provide the isolating mechanisms. But for free swimming or free floating marine animals isolating mechanisms operate through the discreteness of water masses. Brinton's work (1962) serves as an example. He showed not only a correlation of his pelagic euphausiids with separate water masses and oceanic circulation patterns but discussed the possible evolutionary significance of changes in those patterns. The pelagic larvae of spiny lobsters are similarly dependent upon oceanic patterns for their survival and eventual return to the region occupied by the parent stock.

The differences between these water masses are quite well recognised by oceanographers and animals alike; in fact oceanographers can identify and even age a particular part of the water column by its physical and chemical characteristics. On this basis, the Indian, Pacific, Atlantic and Antarctic Oceans are very distinct indeed.

Coastal animals, whether free swimming or bottom living, have their basic oceanic environments markedly influenced by the adjacent land. Sediments of particular sorts are carried by wind or river into the coastal waters, salinity will be altered by adjacent rivers (lower salinities) or by adjacent deserts (higher salinities) and the local water circulation pattern is determined by the coastal configuration. One wonders what the biological effects will be when the Central American Seaway is completed. Rubinoff (1968) has proposed the biological problem and has pointed to many of the differences between the Atlantic and Pacific coastal waters of Central America.

Figure 1b shows a section through the coastal shelf indicating the factors influencing the region occupied by the bottom dwelling spiny lobster. All these factors vary in amount with time and the combinations of these factors produce the seasonal marine climate for a particular animal. For coastal animals, there are seasons of rainfall and drought on the adjacent land which vary the run off into the sea and there are similar seasons of oceanic water circulation; changes in the position, direction or intensity of flow of a current will seasonally affect the environment of a fixed or slow moving bottom living animal. Also seasonal solar variations produce regular changes in food resources via plankton activity. Such short term seasonal changes are analogous to the conditions which are found on land and which form the terrestrial climate.

Environmental change

In the past, however, the magnitude of changes has been much greater than those we observe today as seasonal events. All the marine climatic factors illustrated in Figure 1b would have been affected by changes in the position of wind belts, oceanic circulation, upwelling, exchange of

TABLE 1
Distribution of water "types" compiled from the vertical sections of temperature and salinity given in Marshall 1958 pp. 53 and 55 for Western Atlantic Ocean

Approximate depth range (metres) and marine zone	Approximate percentage of total volume	Temperature °C	Range °C	Salinity ‰	Range ‰
Surface—250 Subtropic and Tropic	3	>20	16	30-37	7
Subsurface—1000 Subpolar and Temperate	11	4-20	16	35.0-36.0	1.0
1000-4000 Antarctic Cell 500-4000 } Polar	75	1-4	3	34.6-35.0	0.4
	11	<1	2	<34.6	very small

oxygen at the surface, evaporation, terrestrial run-off and sedimentation. The importance of solar radiation as the prime controller of the climate in the sea and on the land must be stressed and I submit that through this control, solar radiation is and always has been the key factor in determining the distribution and speciation of animals on the earth.*

When attempting to evaluate what the response of marine species might have been to environmental changes in the past, it is very important to have some concept of the relative stability and geophaphic extent of the water mass inhabited by the species under consideration. In Table 1 the proportions by volume of

waters with selected characteristics of salinity and temperature have been assessed. On the percentage by volume, the proportion of the tropical and subtropical waters is very small indeed—only 3%. The combined temperate and subpolar waters are about 11% but the polar waters are 86% of the total, part of which (about 11%) can be clearly recognised as Antarctic water. Any changes that occur to the earth's environment must affect the relatively small volume of surface waters of the tropics and subtropics much more quickly and to a greater degree than the large volume of the subsurface waters.

Climate and spiny lobsters

Figure 2 illustrates the Australian climatic regions, the Australian coastal sedimentation zones and the distribution of the marine spiny

*One of the most illuminating studies on long-term variation in solar radiation takes into account past changes in the spatial distribution of earth, sun and moon (Steiner, 1967).

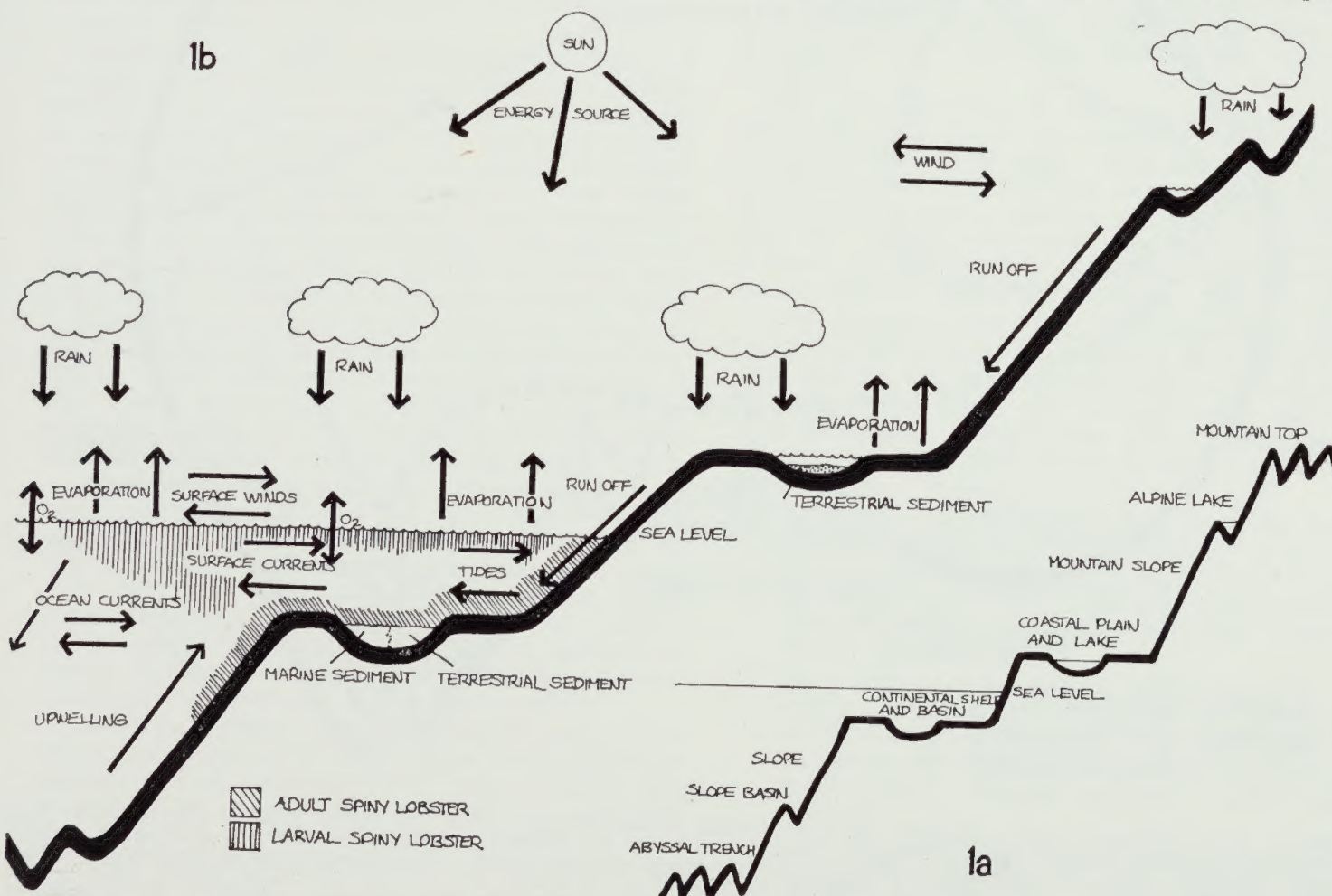


Figure 1.—Comparison of terrestrial and submarine conditions. 1a. Diagrammatic section showing some analogous situations above and below sea level. 1b. The influence of climate on marine habitats with particular reference to the coastal and shelf regions inhabited by spiny lobsters.

lobsters in the coastal waters; a correlation of major zones is readily observed. Approximate localities where the most rapid change occurs are Frazer Island (Queensland), Bass Strait (Tasmania), and North West Cape (Western Australia). At these places major changes occur in climate, coastal sedimentation and species composition of spiny lobsters.

There are also minor but significant breaks in the patterns at Derby in the north west of Western Australia characterised by climatic change and an apparent "barrier" to the westward movement of a spiny lobster *P. polyphagus*. The break at the south west corner of Australia (about Cape Leeuwin) is signified by the meeting of two spiny lobster species *P. cygnus* and *J. novaehollandiae*. This is probably a reflection of the coastal marine seasonal conditions of the west coast which has subtropical north flowing ocean currents in the summer and in the winter the development of a south flowing wedge

of tropical ocean water which extends from the north to about Cape Leeuwin. The distribution of marine coastal animals around Australia is determined by such combinations of basic oceanic water type, extent of terrestrial run off, sedimentation from the land and the nature of the land which is being eroded.

It is noteworthy that the combinations of environmental factors as indicated in Figure 2 fit remarkably well with the generally acceptable marine zoogeographic provinces of Australian coasts (Kott 1952, Bennett and Pope 1953, Endean 1957). Along the Pacific Queensland coast the effects of local climatic conditions have resulted in the recognition of two faunas—the coastal Banksian which is influenced by the terrestrial mud and the Solandrian which is offshore, clear of the mud, where the clear waters and coral reefs of the Great Barrier Reef provide the basic environment.

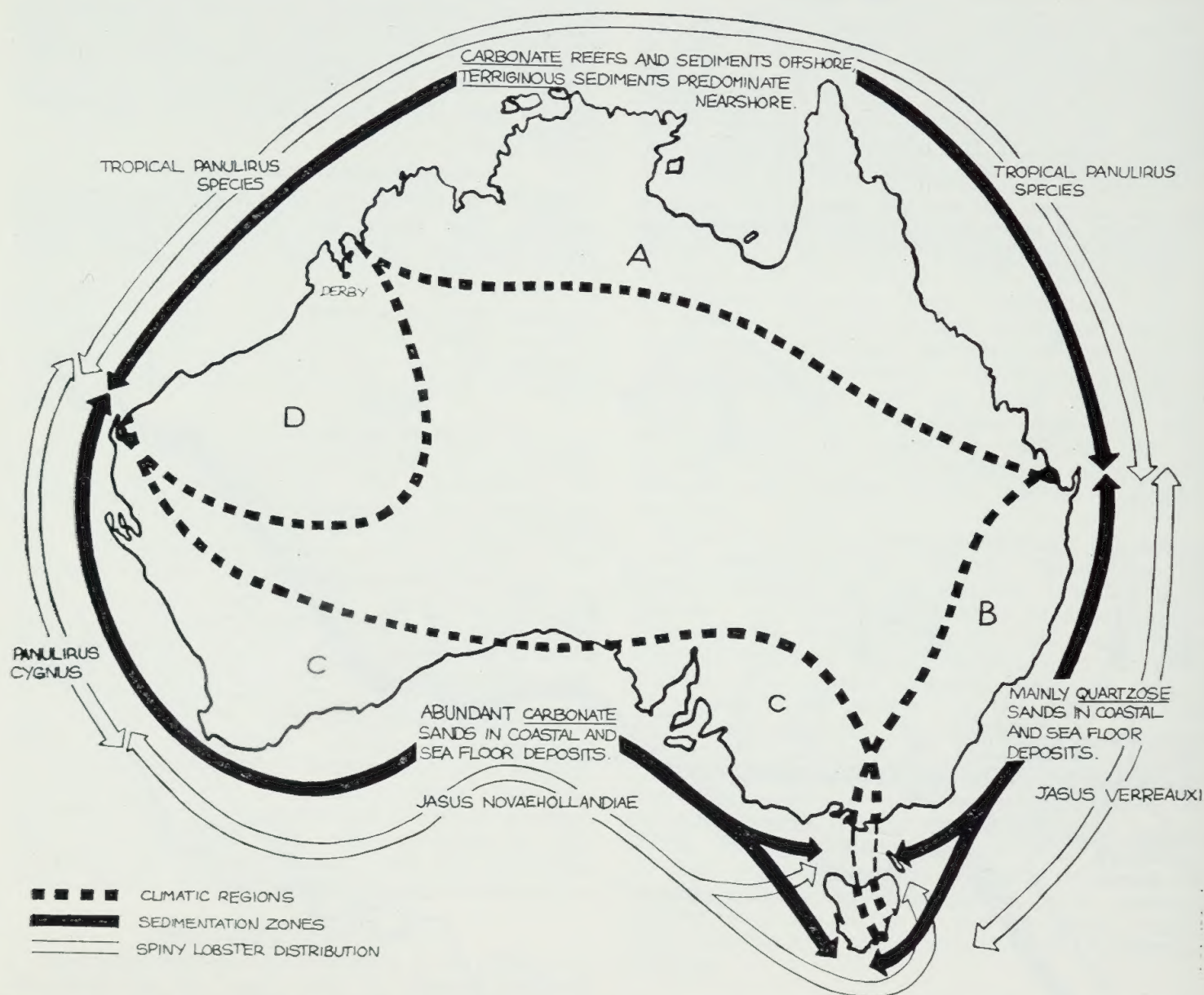


Figure 2.—Australian coastal climatic regions, coastal sedimentation zones and spiny lobster distribution. The types of sedimentation on the Australian continental shelf are taken from Brown (1968). The climatic regions were compiled from Thornthwaite (1931) (in Keast, 1959), Gentili (1961) and Commonwealth Bureau of Census and Statistics (1966). The regional climatic classification is based on rainfall character which reflects the rainfall throughout year, reliable; C. Rainfall predominantly winter, reliable; D. Rainfall during summer cyclones, winter dry, very unreliable. Note: Derby appears to be about the westward limit of *P. polyphagus*, one of the tropical *Panulirus* species.

Now let us look at the broad marine zoogeographic faunal zones described so well by Ekman, selecting again for our examples the spiny lobster. The zones for shallow water animals are the tropic, subtropic, temperate (all of which have spiny lobsters living in them) subpolar and polar. (Spiny lobsters also occur in subpolar regions but only as deep water species in depths down to 700 fathoms.)

The tropical northern Australian spiny lobsters are not endemic to Australia but form part of a vast fauna which is called the Indo-West Pacific fauna (Ekman, 1953). Many animals apparently have little difficulty in dispersing, either as adults or larvae, all along the extensive continental and island coasts of the Indian and western part of the Pacific Ocean. These tropical shallow water species are distinct from, but nevertheless quite similar to, the spiny lobster species in three equatorial faunas—the East Pacific, the West Atlantic and the East Atlantic (which extends to some degree into the Mediterranean).

The subtropic species of spiny lobster in Australia live along the west coast (*Panulirus cygnus*) and the lower east coast (*Jasus verreauxi*). *P. cygnus* is an Australian endemic and is closely related to other endemic subtropic Indo-West Pacific species in Japan (*P. japonicus*), Hawaii (*P. marginatus*), Easter Island (*P. pascuensis*) as well as the equatorial *P. longipes*. *J. verreauxi* occurs in the north island of New Zealand as well as the New South Wales coast and represents as a single species a distinct subgroup of *Jasus*.

On the south coast of Australia the fauna is mostly unique to Australia although very similar species occur on the other continents and islands at equivalent latitude in the southern hemisphere. The southern crayfish *Jasus novaehollandiae* is very closely related to the other *Jasus* species in New Zealand, Juan Fernandez, Tristan da Cunha, South African west coast, and St. Paul Islands. These species of *Jasus* form part of the circumpolar temperate marine fauna.

Although species of spiny lobster do not occur on the Subantarctic Islands to the south of Australia, clear faunal zones occur in these waters. On these Subantarctic Islands a circumpolar subpolar fauna is recognised and further south around Antarctica there is a distinct polar fauna.

These latitudinal zones are determined by the physical characteristics of the water masses adjacent to those coastal regions, modified by any particular influences of the local land mass. One of the most obvious and most easily measured physical features of these water masses is the water temperature and the boundaries of these marine zones are usually defined by zoogeographers by water temperature values.

Vaughan's (1940) proposed marine zones were based on temperature and these zones certainly correlate with distribution of spiny lobster. But temperature as such does not serve to separate the 6 species of tropical spiny lobsters as temperature appears to separate the subtropic and temperate species.

Vaughan's zonation applied to the Australian and other regions mentioned above is as follows:

Polar	-1.9 to 5°C	Antarctic.
Subpolar	5 to 10°C	Subantarctic.
Temperate	10 to 25°C	South coast of Australia (1 sp. of spiny lobster).
Subtropic	15 to 30°C	West and lower east coast of Australia (1 sp. of spiny lobster in each area).
Tropic	25 to 31°C	North coast of Australia and Indo-West Pacific (6 spp. of spiny lobster).

So far we have been dealing only with the spiny lobsters in the shallow coastal waters, but they also show very clear evidence of vertical and latitudinal zonation as well (see George & Main 1967 Fig. 2). The vertical zonation broadly correlates with water temperature but once again we must note that temperature is a reflection of the total water mass the species lives in. For instance oxygen availability is probably far more important than actual temperature to marine animals whether in the deep sea or in the shallow waters. The sources of oxygen for the deep sea are in several specific surface regions of the oceans, i.e. north west Atlantic, Weddell Sea and other regions around Antarctica.

In those places, oxygen values are highest; the lower the value in the deep sea the "older" the water is thought to be. On this basis the "oldest" water is in the North Pacific, i.e. the oxygen has been used up by biological processes in its passage from the regions of the Antarctic to the North Pacific. Oxygen requirements for any one of the spiny lobster species is not known but whatever their requirements are, the evolutionary selection has been initiated by the very nature of the waters to which they are now adapted.

The next question is why are there so many *Panulirus* species in the shallow tropic regions compared with subtropic? This applies not only to the *Panulirus* group but as a general rule to all marine groups. Species diversity is a reflection of habitat diversity and the equatorial shallow water region certainly provides very many different sorts of habitats.

The following examples will adequately illustrate the wide range of habitats, determined for any region by the combination of the local oceanic water mass, the local climate and the local geography and geology. The region I have chosen is the Indo-West Pacific equatorial region.

1. Red Sea—barred deep basin with little water exchange with the Indian Ocean. Adjacent deserts and low river run off result in little sediment on coastal shelf and high evaporation. So waters are clear, warm and probably above normal salinity.
2. East Aden—open ocean with seasonal low water temperature because of upwelling. Waters clear in non-monsoon but very turbid in monsoon. Substrate fine sand of terrestrial origin. Normal salinity. Little coral growth.
3. Indian west coast—open Indian Ocean coast flooded in the northern part by the Indus River resulting in a trend from north to south from a muddy, seasonally flooded area to fairly clear, low run off area in the south.

Evolution of Palinuridae

4. Bay of Bengal—well established large rivers drain continuously from the Himalayas via the Ganges, the Irrawaddy and Brahmaputra Rivers. Salinity of the whole bay is very low (normal sea salinities are not met with until about south of approximately 10°N latitude). The huge volumes of sediment carried by the rivers make the bay more like a huge, deep silty estuary.
5. Arafura Sea, Gulf of Carpentaria and Timor Sea—these regions together form a semi-enclosed, shallow region, narrowly open to the east through Torres Strait and broadly open to the west. Moderate volumes of sediment and fresh water discharge result in a reasonably muddy marine environment, subject to regular flooding of the coastal rivers with some flow of oceanic water from the Pacific via Torres Strait.
6. Offshore islands—some terrestrial run off into the shallow waters and beyond the influence of the rivers, fringing coral or limestone reefs in crystal clear water. This is essentially the condition found along the Queensland north coast already mentioned, i.e. muddy coastal waters and clear coral waters offshore.

These examples illustrate the contrasts in habitat provided in this equatorial region of fairly uniform water temperature. But we see that in spite of these fairly uniform water temperatures different yet reliable habitats are present. An assessment of the degree of reliability of a habitat is paramount in the full understanding of past evolutionary events in the "life" of a species.

Now where do the tropical species of *Panulirus* fit into these habitats? In the Red Sea *P. penicillatus* predominates in those clear waters. In East Aden one species, *P. homarus*, dominates in the cooler, slightly turbid waters. In the very muddy coastal waters off Karachi, *P. polyphagus* is the most common species and as one proceeds south along the west coast of India other species dominate. The order of relative abundance proceeding south is *P. polyphagus*, *P. ornatus*, *P. homarus*, *P. versicolor*, *P. longipes* and *P. penicillatus*. The very low salinity waters of the Bay of Bengal have few records of crayfish at all; the only records of note are from the Andaman and Nicobar Islands which are well offshore. In the Arafura Sea, Gulf of Carpentaria and Timor Sea to the north of Australia there are probably many more prawns than spiny lobster but one species, *P. polyphagus*, appears to be the most common spiny lobster. It has been trawled in low numbers in Joseph Bonaparte Gulf. Records of other species of spiny lobster in Western Australian northern waters follow the habitat trend in turbidity illustrated on the west coast of India. These results have been published recently (George 1968). In the offshore islands of the Pacific, *P. penicillatus* and *P. longipes* are the main species in the clear waters with some occurrences of *P. ornatus* or *P. versicolor* if enough of the right kinds of sediment is available.

For many of the extant palinurids, environmental changes have resulted in little radiation even though they are relatively old groups. George and Main (1967: 813) suggest that for these deeper water primitive groups "the geological and oceanic barriers which divided the once continuous equatorial seas of the world (including the Tethys Sea) into the present day faunal regions fragmented the early stocks, and that the subsequent morphological changes in these groups were very slow". For the deep water genus, *Puerulus*, for example, living in the isolated deep water basins, each of which probably has a peculiar environmental character, one can imagine the difficulty of altering the oxygen content or the temperature or the salinity or the substrate without a major upheaval of the ocean's circulation patterns.

We can more easily imagine changes which would influence the evolution of a more recent (but not the most recent) group like *Jasus*. This genus is at least as old as the lower Miocene (Glaessner 1960) and the evolution of this circumpolar group of species is best explained by shifts of the southern circumpolar temperate belt into higher latitudes. Such a shift would alter the geographical position (but not necessarily the physical characteristics) of the marine temperate zone as recognised today. Six species live in this zone; on the south coast of Australia (*J. novaehollandiae*), New Zealand (*J. edwardsi*), Juan Fernandez (*J. frontalis*), Tristan da Cunha (*J. tristani*), south west coast of Africa (*J. lalandii*) and St. Paul's Island (*J. paulensis*). A very distinct species, outside this group of species, lives on the New South Wales coast and in the north of the North Island, New Zealand—*J. verreauxi*.

There is good evidence of much warmer conditions prevailing in the past. Cowen summarises (p. 182) the earth "has been relatively warm and moist throughout much of geological time. For 90 per cent of the past half billion years . . . its average surface temperature has been 72° Fahrenheit in contrast to the present average temperature of 58°. Tropical and subtropical climates prevailed to high northern and southern latitudes".

How might the present species of *Jasus* have originated? In warmer times the parent species of the *Jasus* group would have been much further south, occupying a circumpolar distribution in the present geographic position of the Subantarctic Zone. The present Subantarctic Zone lies between about 45-55° S. latitude and a fairly uniform marine fauna is recognised on the coasts of these islands and continents. Powell (1965 p. 352) for instance describes three major marine provinces for molluscs within the Subantarctic.

The Magellan: Patagonia west coast to Chiloe I., east coast to C. Blanco and the east Patagonian Continental Shelf including Falkland Islands and Burdwood Bank.

The Kerguelenian: Kerguelen, Crozet, Marion, Prince Edward and Macquarie Islands.

The Antipodean: Auckland, Campbell, Antipodes and Bounty Islands.

This would have been the approximate geographical distribution of the parent *Jasus* species and the water would have been temperate in character rather than subpolar. The West Wind Drift was probably still present but perhaps weaker than present and in those latitudes it would be a suitable transport mechanism for the pelagic larvae especially if they clung to flotsam. Large seaweed rafts float eastward under the influence of the West Wind Drift and are characteristic of these latitudes today.

With a general cooling, i.e. a shift to lower latitudes of waters with today's temperate environment, geographic isolation of the parent *Jasus* stock would be likely on the coasts of the southern continents and on mid latitude island groups. Natural selection would operate against very long larval life under these conditions and a shortening of the larval life would become an advantage. The possible pathways which lead to these isolations would be influenced by the direction and strength of the currents, the availability of relatively shallow water and the length of larval life. Isolation is envisaged as follows:

- (a) the *frontalis* population moving northward up the west South American coast, responding to the present northward sweep of the West Wind Drift up the South American coast and responding to the selection pressures of the "marine climate" of the St. Ambrosius-Juan Fernandez region
- (b) the *lalandii* population moving north and east via the Mid Atlantic and Walvis Ridges to the west coast of South Africa, responding to the northward sweep of the West Wind Drift up the South African coast. It is now responding to the regular marine environment produced by the Benguela Current.
- (c) the *tristani* and *paulensis* populations moving to the north via the Mid Atlantic, the Atlantic-Indian and the Mid Indian Ridges under the influence of northerly offshoots of the West Wind Drift.
- (d) from the Macquarie Antipodean region, the *novaehollandiae* population migrating to the south coast of Australia via the South Tasmanian Ridge and the *edwardsi* population taking up their present position on the main islands of New Zealand and Chatham I. by way of the Campbell Plateau. The major selective factors which maintain isolation of these two species today are the distinctive bottom substrates and patterns of water circulation around southern Australian and New Zealand coasts.

The other species of *Jasus* (*J. verreauxi*) which today lives in subtropic temperatures probably always occupied a geographic position in waters to the north of the *J. lalandii* group just discussed. Indeed a lower Miocene fossil remarkably close to *J. verreauxi*, (*J. flemingi*), has been recorded from Nelson in New Zealand, a locality much further south than the present day distribution of *J. verreauxi* (Kensler 1968). Perhaps at that time the *J. verreauxi* parent species occupied the present geographic range of *J.*

edwardsi when the *J. edwardsi* parent species was further south on the New Zealand subantarctic islands.

In the equatorial warm waters, one genus *Panulirus* is dominant and radiation has been the most rapid and the most recent of all palinurids (George and Main 1967). These workers have pointed out that in the Cretaceous and early Tertiary similar radiations of spiny lobsters occurred as evidenced by the abundant shallow water fossils of *Linuparus* for example. The simplest explanation for the rapid evolution of species in these tropical regions is to have development of "new" habitats. Geographic areas in the tropics are the most likely to have changing habitats with slight changes in climatic conditions and with these changes "new" habitats can form. We have seen how some of these geographic regions—Red Sea, East Aden, Indian west coast, Bay of Bengal, and Arafura Sea-Gulf of Carpentaria-Timor Sea region have their characteristic habitats maintained under the present climatic conditions. And we have also seen how the separate species of *Panulirus* in the Indian and West Pacific Oceans preferentially occupy these habitats. It is suggested here that those habitats are of relatively recent origin (perhaps with the warming of the waters after the Pliocene) and that the fluctuations of climate and ocean currents during the Pleistocene have resulted in contractions and expansions of species range and isolations and reconnections across ocean "barriers" and terrestrial isthmuses.

If the present day region of most suitable habitat for a species was in fact its geographic origin, I venture the following suggestions for the tropical *Panulirus* species of the Indo-West Pacific. *P. penicillatus* was originally isolated in the Red Sea and that natural selection operated in favour of individuals best adapted to clear water unaffected by organic or terrestrial sediments. *P. homarus* arose off the west coast of the Arabian Sea in response to the proximity of the oceanic, cooler waters caused by coastal upwelling and the nature of the terrestrial sediments. *P. ornatus* may have evolved along the East African coast in response to the conditions determined by the particular nature of the organic sedimentation there. *P. polyphagus* with its affinity for river mud could have initially separated in response to the Indus system which is reasonably reliable in character since it originates in the Himalayas. *P. versicolor* could have originated in a warm water area adjacent to live coral areas but not necessarily in the live coral itself. These conditions prevail on the north coast of Western Australia between Roebourne and Broome where sediments from the Great Sandy Desert blow into coastal waters and where tidal movements stir up these sediments (see George 1968).

If these origins are correct then distributions of species to regions outside these main centres occur where similar environmental conditions exist. When a period of climatic change stresses the species, the species range would be expected to contract towards the most ideal (and presumably the original) geographic region. Periods of expansion would also be expected if suitable habitats are provided in additional areas. But

a change in one set of climatic conditions may result in expansion of one species but adversely affect other species which would contract their range. Increased rainfall and sediment discharge would expand the range of *P. polyphagus* near the rivers but would cause *P. penicillatus* (Red Sea) to contract its range since the waters would contain more terrestrial sediment.

Conclusion

The state of knowledge about the distribution, taxonomy, ecology and phylogenetic interpretation of marine animal groups is not as complete as for the terrestrial groups. Nevertheless, the same principles of isolation and subsequent speciation must apply and by using marine spiny lobsters as an example I have attempted to suggest how these principles may account for the present distribution of a particular marine group of animals. The effect of environmental change is one of the most important concepts in any explanation of the distribution of both marine and terrestrial animals in space and in time since the total environment (the climate) constantly selects for animals best suited to meet that set of environmental parameters. Changes in climate patterns directly and immediately alter the value of previous selective advantages.

I would like to summarise the opinions I have presented in this paper as follows:

1. A marine climate exists under the sea and this operates in the same manner in the distribution of marine animals as the terrestrial climate operates on terrestrial animals.
2. For the coastal species of spiny lobsters, their marine climate is determined by such factors as coastal morphology, terrestrial rainfall, submarine geology and adjacent terrestrial geology, adjacent circulation of ocean water masses.
3. Combinations of these factors provide numerous distinct spiny lobster habitats, isolated from one another by the regional peculiarities.
4. The coastal habitats in the tropics are much more easily changed by climatic events than coastal habitats in higher latitudes or deep water habitats.
5. In the shallows of the tropic region, speciation is more rapid than in other regions and in this sense is an "origin for species" but not a centre from which these species are despatched to other regions with different environments.
6. Evolutionists must assess the biological attributes which natural events have selected in the past evolution of the species examined so that the most likely means of isolation for their studied species can be proposed.
7. *Jasus* species probably became geographically separated on the coasts of the southern continents and islands after the stock (as one circumpolar species in the present Subantarctic region) moved north to the lower latitudes with a climate cooling.

Acknowledgements

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8.—Upper Eocene Planktonic Foraminiferida from Albany, Western Australia

by Patrick G. Quilty*

Manuscript received and accepted 18 February 1969

Abstract

A sample of 2500 planktonic foraminifera from the Nanarup Limestone Member of the Plantagenet Group at Nanarup, near Albany, on the south coast of Western Australia has yielded 22 taxa (form, species, etc.) of which *Globanomalina micra* (Cole), *Globigerina ampliapertura* form *ampliapertura* Bolli and *Globigerapsis index* (Finlay) are dominant, the latter making up 60% of the planktonic fauna. *G. index* is discussed in some detail, and statistical analysis of 436 specimens indicates that such generic names as *Globigerinita*, *Catapsydrax* and *Globigerinoides* must be used on a more restricted basis than at present, and that *Globigerinatheka*, *Globigerinatella*, *Globigerinoita* and *Inordinatosphaera* must be rejected. *Globigerina ciproensis* form *basaapertura* and *G. jenkinsi* are described as new. The warm water fauna is Upper Eocene in age.

Introduction

The Plantagenet Group is mentioned (as the Plantagenet Beds) in numerous publications, most of which deal with mineral resources of Precambrian inliers, water or petroleum possibilities in the sediments, and the general geology of small areas within the major development.

The history of the study of the Plantagenet Group prior to 1954 is well presented by Clarke and Phillips (1954) and will not be repeated here. Until 1954 the only well preserved fossils studied were sponge spicules and the accepted age of the sediments at that time was Miocene.

Singleton (1954) seems to have been the first to dispute the Miocene age, considering the sediments to be Upper Eocene because of the occurrence of the nautiloid *Aturia clarkei* Teichert, elsewhere of Upper Eocene age. Palynological investigations by Balme and Churchill (1958), indicated a Lower Oligocene or Upper Eocene age for the 400 feet of sediments in Rollo's Bore, Coolgardie, which have been correlated with the Plantagenet Group. They conducted their studies on the only other well preserved fossils apart from the sponges. Glenister and Glover (1958) also gave a Middle or Upper Eocene age on the basis of the nautiloid *Teichertia prora*. McWhae *et al.* (1958) and Glaessner (*in* Lotze, 1959) also quoted an Upper Eocene age, probably on the basis of the nautiloids, but Sofoulis (1958) still used the Lower Miocene age. Hodgson, Quilty and Rutledge (1961) did the first detailed study on a part of the Plantagenet Group. The area studied was mainly Cape Riche, 70 miles east of Albany, but foraminifera and echinoids from Nanarup near Albany, were also examined and formed the basis for an Upper Eocene age determination. Wyatt (1962) in his search for commercial lime deposits in the Albany district took a sample (his sample No. 13026) from the lime quarry at Nanarup from

which also comes most of the material studied for this paper. He apparently mistook it for the Coastal Limestone so prevalent on this coastline. Kay *et al.* (1963) quoted my 1961 (*in* Hodgson, Quilty and Rutledge, 1961) Upper Eocene determination based on foraminifera. Cockbain (1967) reported *Asterocyclina* from Neridup, near Esperance.

The limestone at Nanarup contains an extensive fauna of foraminifera, echinoids and bryozoa with many brachiopods, pelecypods, gastropods, occasional fish teeth, nautiloids and associated calcareous algae.

The locality of the Nanarup quarry is shown in Figure 1. The coordinates of the quarry are:

Latitude—34° 58' 47"S.

Longitude—118° 02' 12"E.

Rock specimens and foraminifera identified herein are housed in the collection of the Geology Department, University of Western Australia, and the number following the symbol U.W.A.G.D. represents the number of the specimen in that collection.

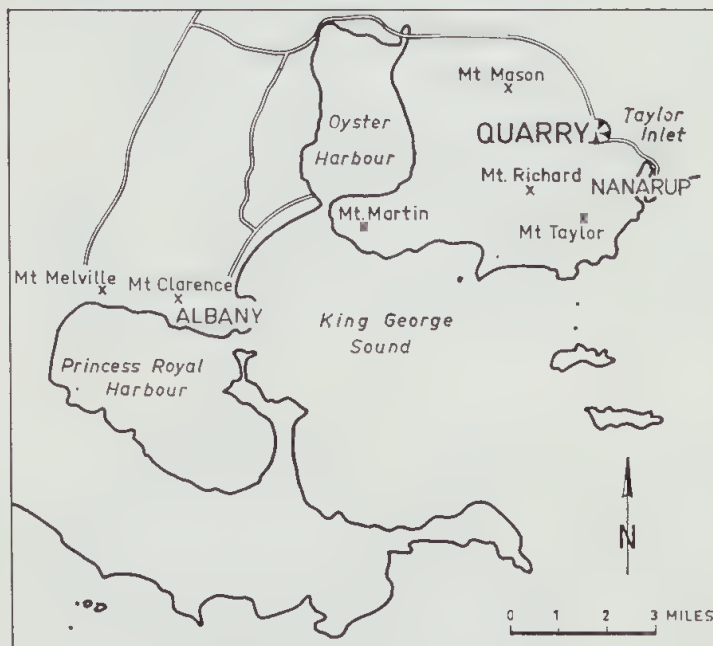


Figure 1.—Locality map.

Several spellings of the locality are in existence. The Military Survey Mt Manypeaks (No. 478) Map sheet has the name spelled Nannarup. The same series Albany (No 480) Map sheet has the name spelled Nannerup, and the latest road map put out by the Ampol Petroleum Co. spells it Nanarup. The Nomenclature Advisory Committee of the Western Australian Lands and Surveys Department advises me that the latter spelling is correct and it is adopted here.

* Geology Department, University of Tasmania, Hobart.

The limestone at Nanarup

The limestone (actually an almost unconsolidated bryozoal calcarenite) is lithologically very different from most other rock types so far recorded from the Plantagenet Group and it is desirable to show that it is in fact, part of those sediments.

The limestone is Upper Eocene in age. Other areas of the Plantagenet Group are also Upper Eocene in age, this dating based on nautiloids (Singleton, 1954; Glenister and Glover, 1958). Thus there is the evidence of age.

The limestone is surrounded by Precambrian basement and has not been seen in contact with other parts of the Plantagenet Group. No structural disruptions are known between the limestone and the Plantagenet Group a few miles to the east. Thus since the limestone and the Plantagenet Group to the east have similar elevations above sea level, it is logical to equate them.

The Coastal Limestone is generally regarded as being quite young (Pliocene (?), Pleistocene—Recent) and is thus distinct. However, the Eocene limestone at Nanarup has been confused with the younger deposit at least once (Wyatt, 1962) and it is necessary to point out the difference. The Coastal Limestone is generally a subaerial calcarenite whereas the Eocene material is marine. The Coastal Limestone is composed commonly of at least 50% rounded, well sorted wind blown quartz sand, whereas the Nanarup deposit has a very high calcium carbonate content and any detrital fragments found in the sediment are angular, poorly sorted rock fragments often containing quite fresh feldspar. The younger deposit is usually characterised by cross bedding whereas the Eocene sediment is essentially unbedded.

The extent and thickness of the limestone is unknown. The area known covers only about 25 acres and the maximum thickness is about 15-20 feet. Cockbain (1968) formalised the nomenclature, naming the limestone as the Nanarup Limestone Member of the Werillup Formation. McTavish (1966) had referred invalidly to the Nannarup Limestone.

Systematic descriptions

Order FORAMINIFERIDA Eichwald, 1830.

Superfamily GLOBIGERINACEA

Nomenclature of planktonic foraminifera

After having examined large populations of *Globigerapsis index* (Finlay) and having had some experience with *Globigerina unicava* (Bolli, Loeblich and Tappan) and its allies, I consider that many planktonic foraminifer genera and species are based on gerontic, reproductive or some such specifically nondiagnostic characters, and as such, have no taxonomic significance, even though they may have some empirical stratigraphical significance. Hence *Catapsydrax*, *Globigerinita*, *Tinophodella*, *Globigerinatheka*, *Inordinatosphaera* etc are possibly all biologically invalid genera, and the species of those genera are generally the same thing as previously described species of genera such as *Globigerina*. The only generic names

used herein are *Globanomalina*, *Globigerapsis*, *Globigerina* and *Turborotalia*. The reasons for dismissal of so many generic names will be shown when I discuss *Globigerapsis index* (Finlay) in some detail.

Present-day workers are splitting planktonic foraminifera into finer and finer subdivisions so that trinomial nomenclature is now almost the rule. By splitting taxa into finer units, we should pave the way for finer and finer stratigraphic subdivisions and correlation. Unfortunately, the good to be obtained from such subdivision is often lost because the taxa are very poorly defined and badly illustrated. Also with so many workers in the field, synonymies become rather large, and often very subjective.

In trinomial nomenclature, the ultimate subdivision is usually termed a subspecies. This term should not be used. The International Commission on Zoological Nomenclature defines a subspecies as—

- (1) a category of the species group subordinate to species; or
- (2) an individual taxon of the category "subspecies".

Neither of the ICZN definitions covers the complex situation which has evolved in naming planktonic foraminifera. "Subspecies" should be retained for parts of species which are separated from one another geographically, climatically or by some factor which can be recognised as constituting a genetic barrier of non specific magnitude, rather than for parts of one continuous interbreeding population, members of which cannot be distinguished from one another until the complete adult form is reached, and which genetically are completely intergradational. *Globigerina euapertura* Jenkins, simply by the addition of a bulla, changes genus and species to become *Catapsydrax unicavus* Bolli, Loeblich and Tappan. This is biologically absurd, so the name *C. unicavus*, having priority, is the name which should be used. However, *Catapsydrax* must then be a junior synonym of *Globigerina*, so the species becomes *Globigerina unicava* (Bolli, Loeblich and Tappan). Some "lumpers" would place *G. ampliapertura* Bolli and *G. unicava* in synonymy with *G. apertura* Cushman.

For some purposes, it is useful to give names to these morphotypic subdivisions of *G. apertura*. These cannot be called subspecies, because what was previously called *G. euapertura* still develops into the nominally different morphological subdivision previously called *Catapsydrax unicavus*. The terms "variety" in the sense of Sylvester-Bradley (1951) or "form" or "forma" in the sense of Wade (1964) or Hofker (1959) seem quite good answers to the problem. The name "variety" or "form" seems to have no ontogenetic, gerontic or reproductive implications, which "subspecies" does. Because Wade and Hofker have both used "forma", it is used here, except that the anglicised version "form" is employed.

The classification adopted here is modified from those of Banner and Blow (1959) and Loeblich and Tappan (1961, 1964) and recognises

only the Families Hantkeninidae, Globigerinidae and Globorotaliidae among the Tertiary globigerinid foraminifera.

Family HANTKENINIDAE

Genus GLOBANOMALINA Haque, 1956

Globanomalina micra (Cole), 1927

Fig. 6, no. I, II

- Nonion micrus* Cole 1927, p. 22, pl. 5, fig. 12.
? *Nonion iota* Finlay 1940, p. 456, pl. 65, figs. 108-110.
Globigerinella micra (Cole); Crespín 1956, p. 31.
Hastigerina micra (Cole); Bolli 1957B, p. 161, pl. 35, figs. 1a-2b.
"*Globigerinella*" *iota* (Finlay); Hornibrook 1958A, pp. 27-29, pl. 1, figs. 22-24.
Globigerina iota (Finlay); Hornibrook 1958B, p. 664, figs. 20, 24.
Pseudohastigerina micra (Cole); Banner and Blow 1959, p. 19, 20, pl. 3, figs. 6a, b, text figs. 4g-i.
Hastigerina micra (Cole); Ludbrook 1961, p. 21.
Globigerina iota (Finlay); Hornibrook 1961, p. 148.
Pseudohastigerina micra (Cole); Blow and Banner (in Eames et al.) 1962, p. 129, 130, pl. 16, figs. E, F, text fig. 9, x-xii.
Globanomalina micra (Cole); Loeblich and Tappan 1964, p. C665, fig. 531, 6-8.
Pseudohastigerina micra (Cole); Wade 1964, p. 274, 279, etc., pl. 1, fig. 5.
Nonion iota Finlay Jenkins 1965B, pl. 2, fig. 9.
Globigerina pseudoiota Hornibrook; Jenkins 1965B, pl. 2, fig. 10.
Globanomalina micra (Cole); Jenkins 1965A, p. 1092.

Remarks

The ultimate chamber of this species is often modified, either much more inflated and larger than the penultimate, or volumetrically part of the normal growth series but with the centre of the chamber displaced proximally to a position closer to the proloculus than it would be if it was part of the normal growth series. In the latter case, the proximal extremities of the chamber cover much of umbilicus. This modified ultimate chamber is probably equivalent to the bulla of other globigerinid species.

One hundred and one specimens of the species are present in the sample. Average maximum diameter is 0.25 mm ranging from 0.17 to 0.32 mm. Approximately two thirds of the specimens have six chambers in the last whorl, one tenth have seven, and the rest have five.

Maximum diameter of figured specimens—

- (a) 0.25 mm
- (b) 0.25 mm.

Repository:

- (a) U.W.A.G.D. 59502
- (b) U.W.A.G.D. 59503.

Family GLOBIGERINIDAE

Genus GLOBIGERINA d'Orbigny, 1826.

Globigerina cf. *africana* (Blow and Banner), 1962.

Fig. 6, No. III, IV.

cf. *Globigerinita africana* Blow and Banner (in Eames et al.) 1962, p. 105, 106, pl. 15, figs. A-C.

Remarks

The identification is tentative as a bulla is absent and the apertural characters are not preserved. Only a single specimen was recovered.

Maximum diameter of figured specimen 0.39 mm.

Repository: U.W.A.G.D. 59505.

Globigerina ampliapertura form *ampliapertura* Bolli, 1957.

Fig. 6, No. V-VIII.

Globigerina ampliapertura Bolli 1957A, p. 108, pl. 22, figs. 5a-7b.

Globigerina cf. *ampliapertura* Bolli; Ludbrook 1961, p. 21.

Globigerina ampliapertura ampliapertura Bolli; Blow and Banner (in Eames et al.) 1962, p. 83, 84, pl. 11, figs. A-D.

Globigerina ampliapertura Bolli; Wade 1964, p. 274, 279, pl. 1, figs. 13-15, 17, 18.

Globigerina ampliapertura Bolli; Jenkins 1965A, p. 1092, fig. 2.

Globigerina ampliapertura Bolli; Taylor 1966, p. 33.

Globigerina ampliapertura Bolli; Lindsay 1967, p. 103, pl. 1, fig. 17.

Remarks. In the sample studied, 382 specimens of this form were obtained. 64% are sinistrally coil and 36% dextrally coiled. Average maximum dimension is 0.34 mm, with a size range from 0.19-0.56 mm. A histogram of maximum diameters in the species is shown in Figure 2.

As many specimens in the sample are bullate, one specimen was sectioned to determine the structure of the bulla. This was also done to specimens of "*Globigerinoides*" *index*. Similar results were obtained in each case. In all bullate forms sectioned, the bulla wall is approximately half as thick as the wall of the chamber preceding it, the pores have a diameter half that of the pores in the preceding chamber and the pores are much more closely spaced than in the preceding chamber.

Measurements taken on the section of *G. ampliapertura* are given below.

Wall thickness—

- Bulla 10-13 μ
- Preceding chamber 20-23 μ

Pore spacing—

- Bulla 5-7 μ
- Preceding chamber c.10 μ

Pore diameter—

- Bulla c. 1 μ
- Preceding chamber 2-3 μ

When one examines the histograms of maximum diameters of this species, it is evident that all bullate forms are restricted to a group lying to the right of the depression in the curve. That is, overall, the bullate forms are larger. Two possibilities immediately present themselves.

- (a) The species may be dimorphic,
- (b) The bulla may simply grow on large specimens and be a gerontic chamber.

If the species does exhibit dimorphism, it is probable that the bulla has something to do with the reproductive cycle, the larger specimens being possibly microspheric (see later, under *Globigerina* *index*). Maximum diameter of figured specimens (a) complete specimen 0.40 mm.

- (b) section 0.51 mm.

Repository: (a) U.W.A.G.D. 59506.

(b) U.W.A.G.D. 59536.

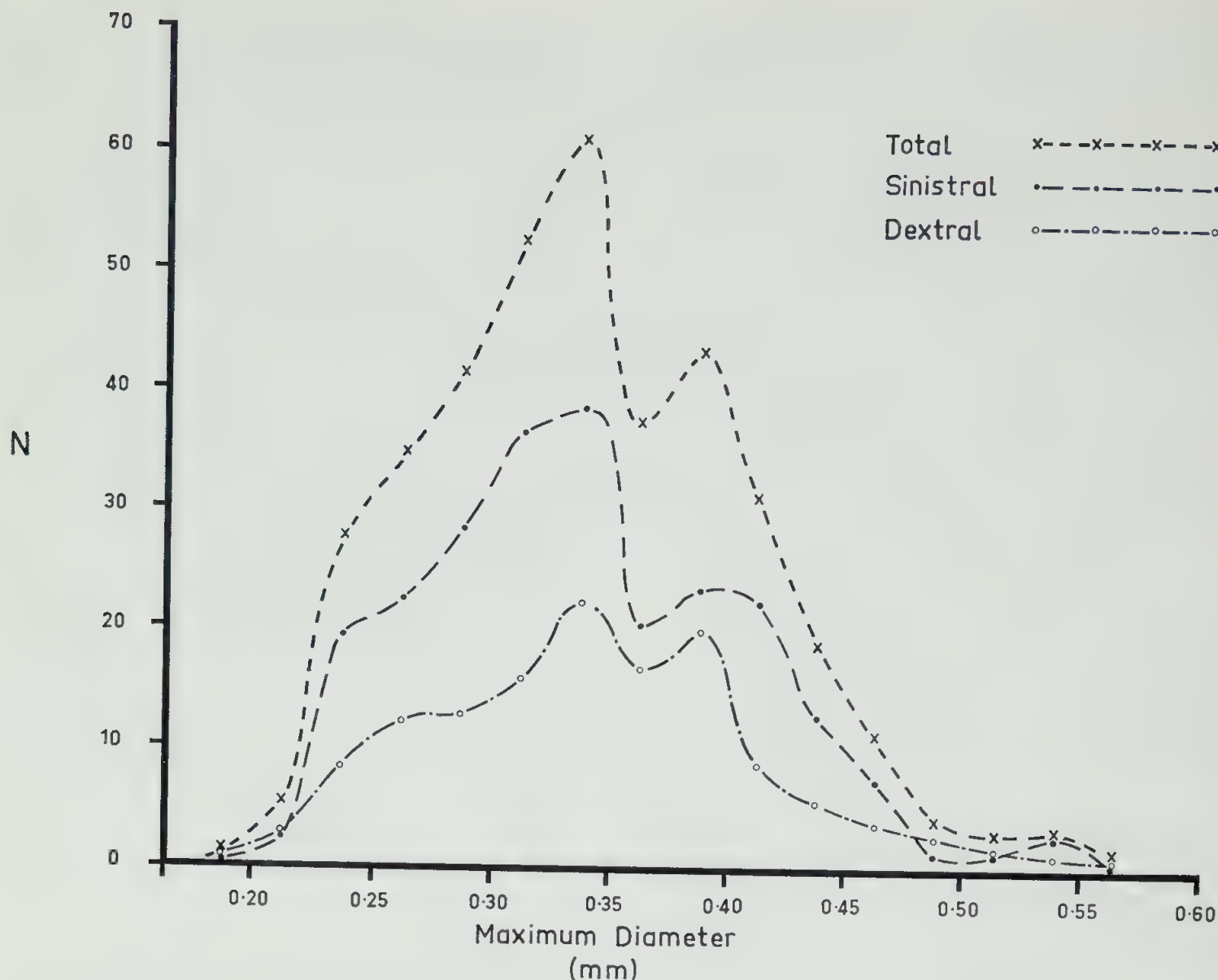


Figure 2.—Frequency curve of maximum diameters—*Globigerina ampliapertura* form *ampliapertura* Bolli.

Globigerina ciperoensis form *angustum-bilicata* Bolli, 1957.

Fig. 6, no. IX-XI

Globigerina ciperoensis angustum-bilicata Bolli 1957A, p. 109, pl. 22, figs. 12, 13; pl. 36, fig. 6.

Globigerina angustum-bilicata Bolli; Blow 1959, p. 172, pl. 7, fig. 33.

Globigerina angustum-bilicata Bolli; Jenkins 1960, p. 350, pl. 1, figs. 2a-c.

Globigerina angustum-bilicata Bolli; Blow and Banner (in Eames et al.) 1962, p. 85, pl. 9, figs. X-Z.

Globigerina angustum-bilicata Bolli; Wade 1964, p. 274, 279, etc., pl. 1, fig. 11.

Globigerina angustum-bilicata (Bolli); Reed 1965, p. 81, pl. 13, figs. 1-6.

Remarks

Apparently unrecorded previously is the occasional presence of bullae in this species. Of 88 specimens seen in this sample, 27 had a well developed bulla. In the sample, 82 specimens (93%) are dextrally coiled and six (7%) sinistrally coiled. Average maximum diameter is 0.25 mm. with a size range from 0.17-0.32 mm.

Maximum diameter of figured specimen 0.21 mm.

Repository: U.W.A.G.D. 59507.

Globigerina ciperoensis form *basaaapertura* Quilty new form.

Fig. 6, no. XII-XV

Diagnosis

Globigerina ciperoensis with $4\frac{1}{2}$ -5 chambers in final whorl, giving a subpentagonal, equatorial profile; distinguished by its size (0.22-0.29 mm.) and low aperture.

Description

Test small, a low trochospire. Subpentagonal in equatorial profile, flat semiovoid in axial. Dorsal surface flat or slightly convex. Periphery strongly lobulate. Surface uniformly hispid with fine granular appearance. Test consists of three whorls of globular chambers, increasing uniformly in size at a rate less than *G. praebul-loides*, or any form except *G. c.* form *ciperoensis*, to which it is similar. First whorl consists of six or seven chambers, last two whorls with $4\frac{1}{2}$ -5 chambers each. Chambers strongly appressed in first whorl but becoming less appressed later. Chambers uniform in shape in last two whorls, with radial and tangential dimensions approxi-

mately equal. Radial sutures straight on both ventral and dorsal sides, more depressed on ventral side than on dorsal.

Spiral suture depressed and lobulate. Aperture a very low arch, between proximal part of penultimate chamber and most ventral posterior part of fifth last chamber; opens into broad deep, irregular pentagonal umbilicus; without lip or rim; apertural face not flattened. Apertures of previous chambers often to some extent continuous with that of ultimate chamber. Ultimate chamber often modified to a small bulla on ventral surface of test.

Remarks

The form is described from a holotype and six paratypes. In the fauna examined, 14 specimens were present, ranging in maximum diameter from 0.22 to 0.29 mm. with an average of between 0.25 and 0.26 mm. Only one sinistrally coiled specimen was seen.

It is similar to *G. c.* form *ciperoensis* Bolli in possessing the same loose growth spiral, surface and wall structures and differs in size, apertural characters and time range. Bolli's (1954) definition of *G. ciperoensis* included a size range of 0.3-0.4 mm. for the maximum diameter of the species and so far I can find no record of this being extended. The aperture of the new form is a low arch whereas that of *G. c.* form *ciperoensis* is a high arch. *G. c.* form *ciperoensis* is not known from Upper Eocene rocks.

G. ciperoensis can be distinguished from *G. ouachitaensis* Howe and Wallace on the basis of number of chambers in the final whorl. The former has about five the latter about four. Thus *G. ouachitaensis gnaucki* Blow and Banner is probably better placed in *G. ciperoensis*. *G. ciperoensis* form *gnaucki* differs from the new form in having a high arched aperture.

G. c. form *angustum-bilicata* Bolli is more involute and has a more restricted umbilicus than the new form. The aperture of the new form is wider and lower than in *G. c.* form *angustum-bilicata*. It also does not possess a lip—a characteristic of *G. c. angustum-bilicata*.

In some respects the growth spiral is similar to that of *Globorotalia postcretacea* (Myatliuk). However, the latter has a much less perforate, smooth test, an apertural lip and a smaller test size (0.12 mm).

It differs from *Globorotaloides suteri* Bolli, in having no globorotaline initial stage. The latter species has been recorded in rocks of this age as close as New Zealand (Jenkins, 1965A) and South Australia (Wade, 1964).

The name is derived from the Latin *basa* (f)—low + *apertura* (f)—aperture or hole.

Maximum diameter of holotype 0.26 mm.

Repository:

(a) Holotype U.W.A.G.D. 59513.

(b) Paratypes U.W.A.G.D. 59514—59518, 60593.

Globigerina (Catapsydrax) cf echinata (Bolli), 1957.

Fig. 6, No. XVI, XVII.

cf. Catapsydrax echinatus Bolli 1957B, p. 165, pl. 37, figs. 2-5.

Remarks

Only two specimens were recovered and thus description as a new species is inadvisable. They are both 0.24 mm. in maximum diameter, one sinistrally and one dextrally coiled.

They are very similar to *G. echinata*, but small sample and poor preservation make accurate identification difficult.

Repository: U.W.A.G.D. 59508.

Globigerina gortanii form *praeturritilina* Blow and Banner, 1962

Fig. 6, No. XVIII-XX

Globigerina turritilina praeturritilina Blow and Banner (in Eames *et al.*) 1962, p. 99, pl. 13, figs. A-C.

Globigerina gortanii Borsetti; Blow and Banner (*op. cit.*) p. 146.

Globigerina praeturritilina Blow and Banner; Jenkins 1965A, fig. 2.

Remarks

As only two specimens of this species were recovered, its variation in the sample is unknown. Of the specimens recovered, one is sinistrally coiled. Both are 0.29 mm in maximum diameter.

The specimens found here are smaller than typical *G. g.* form *praeturritilina*. Also the well defined deep umbilicus is absent. The aperture faces the umbilical position squarely and not slightly obliquely. However, Blow and Banner (1962, *op. cit.*) state that when the umbilicus is less open, the primary aperture is a higher, more semicircular arch, a condition which seems to apply here. No aborted end chamber was seen.

Repository: U.W.A.G.D. 59504.

Globigerina jenkinsi Quilty new species.

Fig. 6, No. XXI, XXII

Diagnosis

Globigerina 0.20-0.30 mm in diameter. Final whorl of three chambers, the aperture of the ultimate chamber sitting symmetrically astride the penultimate and ante penultimate chambers, and with a finely hispid wall with a fine granular appearance.

Description

Test small, a low to moderately high trochospire. Equatorial profile rounded subtriangular, axial profile reniform. Periphery moderately to strongly lobulate. Surface uniformly finely hispid, finely perforate and fairly thin. Ten to twelve chambers arranged in about three involute whorls, five chambers in the first, four in the second and three in the third. Chambers reniform in the early part of the second whorl but increasing very rapidly in size and becoming very globular. Appressed chambers reniform, becoming embracing with the assumption of a globular habit. Spiral suture strongly lobulate, initially very little depressed, but distinctly so at maturity. Dorsal intercameral sutures straight, radial, and little depressed in the first $1\frac{1}{2}$ whorls but becoming curved posteriorly distally and more depressed with the assumption of the globular, embracing habit.

Aperture intraumbilical, variable in shape from a symmetrical small low arch to a small high arch; shared equally by penultimate and antepenultimate chambers; situated in a flattened apertural face and bordered by a poorly to very well developed marginal rim. Umbilicus shallow, triangular and poorly defined. No bulla was seen on any specimens examined.

Remarks

Globigerina brazieri Jenkins is very similar to the new species, the difference though small, being distinctive. The new species is also known as yet only from the Upper Eocene while *G. brazieri* occurs within the Lower Miocene. It is slightly more involute than *G. brazieri*, the aperture is relatively a little lower, and the apertural rim is generally not so distinct. The granular appearance of the wall also seems a little finer.

This distinctive little species has a similar growth form to *G. tripartita* Koch but is distinctly smaller. The latter species appears to have a size range of 0.55-0.75 mm. whereas the new species ranges from 0.20-0.30 mm. with an average value of 0.27 mm. Of the 18 specimens recovered, 15 (84%) are dextrally coiled.

The species is named from a holotype and six paratypes. It is named in honour of Dr. D. G. Jenkins, for his work on Australasian planktonic foraminifera.

Maximum diameter of holotype 0.26 mm.

Repository: (a) Holotype U.W.A.G.D. 59525
(b) Paratypes U.W.A.G.D. 59526-59531.

Globigerina linaperta form *linaperta* Finlay, 1939.

Fig. 6, no. XXIII-XXV

Globigerina linaperta Finlay 1939B, p. 125, pl. 13, figs. 54-57.

Globigerina linaperta Finlay; Hornibrook 1958A, p. 33, pl. 1, figs. 19-21.

Globigerina linaperta Finlay; Carter, 1958B, pp. 50-51, pl. 5, figs. 46, 47.

Globigerina linaperta Finlay; Ludbrook 1961, p. 20, pl. 1, fig. 8.

Globigerina linaperta linaperta Finlay; Blow and Banner (in Eames et al.) 1962, p. 85, pl. 11, fig. H.

Globigerina linaperta Finlay; Wade 1964, p. 274, 279.

Globigerina linaperta Finlay; Jenkins 1965A, fig. 2, p. 1092, etc.

Globigerina linaperta Finlay; Lindsay 1967, p. 105, pl. 1, figs. 23, 24.

Remarks

In this sample, 44 specimens were recovered, of which 26 (60%) are dextrally coiled and 18 (40%) are sinistrally coiled. Average maximum diameter is 0.26 mm. with a size range of 0.20-0.37 mm.

Hornibrook (1958A) refigured the holotype and redescribed the species, noting the fact that a distal flattening of the chambers is a feature of the species. Most descriptions do not mention this distal flattening of the chambers and similarly, few illustrations show it.

Hornibrook (1961, p. 145) gave the time range of *G. linaperta* as Lower to Upper Eocene. He suggested, as did Blow and Banner (in Eames

et al., 1962, p. 87-88), that *G. linaperta* has developed from *G. triloculinoides*. If this is so, it is to be expected that intermediate forms existed before the Eocene rendering distinction between the species difficult and subjective and accounting for much of the confusion.

Maximum diameter of figured specimen 0.27 mm.

Repository: U.W.A.G.D. 59509.

Globigerina martini (Blow and Banner), 1962.

Fig. 6, no. XXVI-XXVIII

Globigerinita martini martini Blow and Banner (in Eames et al.) 1962, pp. 110-111, pl. 14, fig. 0.

Catapsydrax martinii (Blow and Banner); Jenkins 1965A, fig. 2.

Remarks

Of the 16 specimens in the sample, all but one are dextrally coiled. Average size of specimens is 0.25 mm. with a range from 0.20-0.32 mm. Maximum diameter of figured specimen 0.31 mm.

Repository: U.W.A.G.D. 59510.

Globigerina officinalis Subbotina, 1953.

Fig. 7, no. XXIX-XXXI

Globigerina officinalis Subbotina 1953, p. 78, pl. 11, figs. 1a-2c, 6a-7c.

Globigerina officinalis Subbotina; Blow and Banner (in Eames et al.) 1962, p. 88, pl. 9, figs. A-C.

Globigerina officinalis Subbotina; Wade 1964, p. 279, pl. 1, fig. 3.

Remarks: The statement of Blow and Banner (in Eames et al., 1962, p. 88) that the chamber shape in this species is constant, is apparently not quite true. Throughout ontogeny the chambers become more globular and at the same time more appressed. Their illustration (Pl. IX, figs. A-C) shows the change. Another fact not illustrated by them is that the first whorl may contain as many as seven chambers.

Of the 33 specimens in the sample, 29 (88%) are dextrally coiled. Average size is 0.27 mm with a size range of from 0.18-0.35 mm. Maximum diameter of figured specimen 0.30 mm.

Repository: U.W.A.G.D. 59511.

Globigerina ouachitaensis form *ouachitaensis* Howe and Wallace, 1932.

Fig. 7, No. XXXII

Globigerina ouachitaensis Howe and Wallace 1932, p. 74, pl. 10, figs. 7a-b.

Globigerina ouachitaensis ouachitaensis Howe and Wallace; Blow and Banner (in Eames et al.) 1962, p. 90, pl. 9, figs. D, H-K.

Globigerina ouachitaensis Howe and Wallace; Wade 1964, p. 274, etc., pl. 1, fig. 4.

Globigerina ouachitaensis Howe and Wallace; Jenkins 1965A, p. 1091, fig. 2.

Remarks: One of the most characteristic features of the species is the high trochospiral growth form. The Western Australian specimens have a lower trochospiral growth form than the holotype but come close to the holotype spire height and are regarded here as intergradational.

The sample studied consists of 14 specimens of this form, 12 of which are dextrally coiled. Average maximum diameter is 0.28 mm with a range from 0.20 to 0.35 mm. Maximum diameter of figured specimen 0.30 mm.

Repository: U.W.A.G.D. 59512.

Globigerina praebulloides Blow, 1959.

Fig. 7, No. XXXIII, XXXIV

Globigerina praebulloides Blow 1959, p. 180, pl. 8, figs. 47a-c, pl. 9, fig. 48.

Globigerina bulloides d'Orbigny; Ludbrook 1961, p. 19.

Globigerina praebulloides Blow; Blow and Banner (in Eames et al.) 1962, pp. 92-94, pl. 9, figs. O-W.

Globigerina bulloides d'Orbigny; Wade 1964, p. 274 et seq., pl. 1, fig. 6.

Globigerina bulloides d'Orbigny; Jenkins 1965A, p. 1092, fig. 2.

cf. *Globigerina bulloides* d'Orbigny; Lindsay 1967, p. 104, pl. 1, fig. 16.

Remarks

The three forms listed by Blow and Banner (in Eames et al., 1962)—i.e. *Globigerina praebulloides praebulloides*, *G. p. occlusa*, and *G. p. leroyi*—are present although *G. p. leroyi* is somewhat doubtfully identified. While agreeing that they are probably typological forms only, and most probably part of one interbreeding population, I feel that such a subdivision of *G. praebulloides* is worthwhile. Changes in fossil populations of the ratios of the three forms to each other may eventually fulfil the dual roles of (a) aiding accurate interregional correlation and (b) providing an evolutionary series.

In the sample studied the following measurements were noted.

	<i>G. p. praebulloides</i>	<i>G. p. occlusa</i>	<i>G. p. leroyi</i>
Number of specimens	41	42	7
Number (%) of specimens coiled dextrally	35 (85)	40 (95)	7 (100)
Average maximum diameter (mm)	0.28	0.27	0.25

Maximum dimension of figured specimen:

Globigerina praebulloides form *praebulloides* = 0.25 mm.

Repository: U.W.A.G.D. 59519.

Globigerina senilis Bandy, 1949.

Fig. 7, No. XXXV, XXXVI

Globigerina ouachitaensis Howe and Wallace var. *senilis* Bandy 1949, p. 121, pl. 22, figs. 5a-c.

Globigerina senilis Bandy; Blow and Banner (in Eames et al.) 1962, p. 95, 96, pl. 11, figs. R-U.

Remarks: Of 31 specimens recovered, 30 (97%) are dextrally coiled. Average maximum diameter is 0.26 mm with size range from 0.22-0.32 mm. Maximum diameter of figured specimen 0.29 mm.

Repository: U.W.A.G.D. 59522.

Globigerina tripartita form *tapuriensis* Blow and Banner, 1962.

Fig. 7, no. XXXVII-XXXIX

Globigerina tripartita tapuriensis Blow and Banner (in Eames et al.) 1962, p. 97, 98, pl. 10, figs. H-K.

? *Globoquadrina tripartita* (Koch); Jenkins 1965A, fig. 2.

Variation and Remarks

Only two specimens were recovered. They are 0.52 and 0.57 mm in diameter. The larger one is figured.

The specimens found here are very similar to those figured and described as *G. tripartita tapuriensis* by Blow and Banner (*op. cit.*) Their remarks (p. 98) however, would indicate that it should not be found in rocks older than Oligocene. There seems little doubt concerning its identity in this sample. The two samples differ apparently only in that the aperture has no lip in the Nanarup specimens. However, the specimens figured by Blow and Banner apparently does not have one either.

Blow and Banner (*op. cit.*) place *G. rohri* Bolli in synonymy with *G. tripartita* Koch. Dr. H. Bolli has kindly supplied me with topotypes of *G. rohri* Bolli and my specimens appear to represent a different species from the specimens supplied. The wall of *G. rohri* has a more coarsely granular appearance than in the species found here, the early chambers on the dorsal surface are much more distinct, the coiling arrangement is slightly tighter, and there are well developed short spines surrounding the aperture. Blow and Banner (in Eames et al., 1962, p. 96-97) suggested that the spines around the aperture are simply a result of better preservation in this vicinity, similar spines from the entire test surface having been abraded off. I think this explanation an unlikely one, the topotype specimens being apparently quite well preserved with no signs of abrasion. I would thus consider *G. rohri* and *G. tripartita* to be distinct species. Maximum diameter of figured specimen 0.57 mm.

Repository: U.W.A.G.D. 59523.

Globigerina yeguaensis cf form *yeguaensis*
Weinzierl and Applin, 1929.

Fig. 7, no. XL, XLI

cf *Globigerina yeguaensis* Weinzierl and Applin 1929, p. 408, pl. 43, figs. 1a, b.

cf *Globigerina yeguaensis yeguaensis* Weinzierl and Applin; Blow and Banner (in Eames et al.) 1962, p. 99, 100, pl. 12, figs. H-M.

Remarks

G. yeguaensis yeguaensis and *G. y. pseudovenezuelana* are possibly both represented here, but very good preservation in the umbilical region appears to be necessary to distinguish them. The species is rare and apparently not as well preserved as many others here. Most specimens seem closer to *G. y. yeguaensis*.

Nine specimens of the species were found—all dextrally coiled. Maximum diameter ranges from 0.20 to 0.30 mm. with an average value of 0.26 mm.

Maximum diameter of figured specimen 0.26 mm.

Repository: U.W.A.G.D. 59524.

Genus *GLOBIGERAPSIS* Bolli, Loeblich and Tappan, 1957.

Globigerapsis index (Finlay), 1939.

Fig. 7, no. XLII-XLVIII

Globigerinoides conglobata (Brady); Glaessner 1937, p. 29, pl. 1, fig. 3.

Globigerinoides index Finlay 1939B, p. 125, pl. 14, figs. 85-88.

Globigerinoides index Finlay; Finlay and Marwick 1940, pp. 108-111.

Globigerinoides index Finlay; Finlay 1946, p. 240.

- Globigerinoides index* Finlay; Finlay 1947, p. 344.
- Globigerinoides index* Finlay; Dorreen 1948, p. 298, pl. 41, fig. 2.
- Globigerinoides index* Finlay; Grimsdale 1951, pp. 466, 468, 472.
- Globigerinoides index* Finlay; Todd *et al.* 1954, p. 678.
- Globigerinoides index* Finlay; Raggatt and Crespin 1954, pp. 128, 138.
- Globigerinoides index* Finlay; Crespin 1956, pp. 31, 40.
- Globigerinoides index* Finlay; Todd 1957, pp. 268, 270, pl. 70, figs. 5-7.
- Globigerapsis index* (Finlay); Bolli 1957B, p. 165, pl. 36, fig. 16 (? not figs. 14, 15, 17, 18).
- Globigerinoides index* Finlay; Carter 1958A, pp. 297-304.
- Globigerinoides index* Finlay; Carter 1958B, pp. 51, 52, pl. 7, figs. 64-66.
- Globigerinoides index* Finlay; Hornibrook 1958A, p. 34, pl. 1, figs. 11-14.
- Globigerinoides index* Finlay; Ludbrook 1958, p. 110.
- Globigerapsis index* (Finlay); Bermudez 1961, p. 1.251 pl. 8, fig. 6.
- Globigerinoides index* Finlay; Ludbrook 1961, p. 20.
- Globigerapsis index* Finlay; Ludbrook 1961, pl. 1, fig. 9.
- ? *Globigerina linaperta* Finlay; Ludbrook 1961, pl. 1., fig. 8.
- ? *Globigerapsis index* (Finlay); Pessagno 1961, p. 356, pl. 2, figs. 15-17.
- Globigerapsis index* (Finlay); Blow and Banner (*in Eames et al.*) 1962, pp. 124, 125, pl. 15, figs. G-H.
- Globigerapsis index* (Finlay); Wade 1964, p. 274, etc., pl. 1, figs. 9, 10.
- Globigerapsis index index* (Finlay); Jenkins 1965A, p. 1091 *et seq.*, fig. 2.
- Globigerinoides (Globigerapsis) index* Finlay; McTavish 1966, p. 15, etc., pl. 4, figs. 7, 13.
- Globigerapsis index index* (Finlay); Lindsay 1967, p. 105, pl. 1, fig. 19.

Description

Test moderately large (0.25-0.60 mm), globular, a moderately low trochospire. Equatorial profile variable, ovoid to roughly circular to subtriangular. Axial profile ovoid to subovoid. Periphery not lobulate but sharply indented by incised sutures. Surface with coarsely granular appearance. Chambers, in early whorls hard to distinguish due to granularity of surface and even in oils of R.I.=1.62-1.66 only the final two chambers of the second whorl become visible. Glauconitic internal moulds show four chambers in the first whorl, 3½ in second and three in the last. Test of about three whorls of chambers rapidly increasing in size, rate of increase probably greater in last whorl and late chambers of second whorl. Chambers usually globular, but ultimate chamber often only hemispherical or even more flattened. In small specimens ultimate chamber is largest, but in larger specimens it is often smaller than the penultimate. Tangential dimensions of chambers greater than radial. Chambers appressed with incised or "deep cleft" sutures. Spiral suture lobulate in second whorl but not in last, not depressed. Dorsal intercameral sutures nearly straight radial, not depressed but incised. Ventral intercameral sutures incised and straight. In small specimens or those in which last chamber is largest, generally only one aperture, ("Globigerina" type) a small high arch, opening over the antepenultimate—penultimate chamber suture into a very weakly developed umbilicus; usually symmetrical but occasionally markedly asymmetrical with highest point directed posteriorly. Some specimens (mainly those with modified ultimate chamber and some large speci-

mens with ultimate chamber largest) may have two or three apertures often with a marked, thickened, elevated rim. Bullae are developed over each aperture in some specimens.

Variation and Remarks

In the sample studied, 1500 specimens were recovered. A random sample of 436 was tested statistically (see below). Average length (see below) is 0.37 mm with a range from 0.21 to 0.57 mm. Average breadth (see below) is 0.31 mm with a range from 0.18 to 0.47 mm. 95% of specimens are dextrally coiled.

Generic Concepts

In this study, generic differences are established on the following bases (see Figure 3).

(a) "*Globigerina*"—possesses a single umbilical aperture in the ultimate chamber. Ultimate chamber part of the normal growth spiral and normally largest chamber of specimen. [*Globigerina* of Banner and Blow, (1959, p. 5), and Loeblich and Tappan (1964, p. C669)].

(b) "*Globigerinoides*"—as for "*Globigerina*" but the ultimate chamber has two or three apertures—a large, umbilical one and one or two smaller ones on the dorsal side of the test, one always astride the suture of the antepenultimate and fourth last chambers, and another sometimes astride the suture of the penultimate and fourth last chambers. Accessory apertures are rare and difficult to find on chambers previous to the ultimate. [*Globigerinoides* of Banner and Blow (1959, p. 5), Loeblich and Tappan (1964, p. C670) etc.]

(c) "*Globigerapsis*"—differs from the two previous genera in possessing a modified ultimate chamber (see below) situated over the umbilicus of a "*Globigerina*" or "*Globigerinoides*" type individual. More than one aperture is present in this chamber and all apertures are of approximately equal size. The modified ultimate chamber is texturally similar to the preceding chambers of the normal growth spiral (probably Banner and Blow's (1959, p. 6) concept of *Catapsydrax*, and Bolli, Loeblich and Tappan's (1957, p. 33-34) view of *Globigerapsis*, but distinct from Loeblich and Tappan's (1964, p. C676) concept of *Catapsydrax* which has an umbilical bulla and is only questionably distinct from *Globigerinita*).

(d) "*Globigerinita*"—specimens derived from a "*Globigerina*" type by the addition of a single bulla very near to or covering the aperture of the previously formed chamber. The shape, size and position of this bulla vary widely. The bulla is texturally different from the preceding chamber (see below). (Concept essentially that employed by Blow and Banner [*in Eames et al.*, 1962, p. 102-105]).

(e) "*Globigerinatheka*"—analogous to "*Globigerinita*" but developed from a "*Globigerinoides*" or "*Globigerapsis*" type by the addition of a bulla to each aperture of the previously formed chamber. Removal by acid of the bullae and final chamber of a "*Globigerinatheka*" type shows that no bullae were developed before maturity. There may be more than one cycle of bulla development after maturity so that the

aperture of a bulla may in turn have a bulla over it. This concept embraces *Globigerinoita*, *Globigerinatheka*, *Globigerinatella*, and *Inordinatosphaera* as indicated by Banner and Blow (1959, p. 6) Loeblich and Tappan (1964, p. C676-678) and Mohan and Soodan (1967). Jenkins (1965A, fig. 2) included *Globigerinatheka barri* Bronnimann in *G. index* as a subspecies.

In the sample, "genera" occurred in the ratio "Globigerina": "Globigerinoides": "Globigerapsis": "Globigerinita": "Globigerinatheka": 45:9:10½:7:1.

Statistics

To test the hypothesis that the "generic" groups are conspecific, a sample of 436 specimens was analysed statistically. For each specimen, two measurements were made. (See Figure 3 for explanation.)

(a) the length (L) taken as the maximum distance from the distal extremity of the ultimate chamber in the normal growth spiral to the distal extremities of the antepenultimate, and penultimate chambers in a line through the umbilicus. In "*Globigerina*" and "*Globigerinoides*" types this is the maximum dimension of the specimen. In other generic types, the final chamber, not being part of the normal growth spiral, is not considered, and the measurements are taken on the largest part of the test formed as a normal growth spiral.

(b) the breadth (B) taken as the maximum diameter at right angles to L, both L and B measured in a plane perpendicular to the axis of the growth spiral (see Figure 3).

The measurements L and B are considered significant, as any change of spire characteristics will make itself evident in these measurements.

Graphs of L against B and the calculated lines of best fit for each generic type, and

G. index overall are presented in Figure 4. The superimposed lines of best fit are presented in Figure 5.

The measurements were analysed according to the method outlined by Imbrie (1956) and his symbols are used throughout.

Most of the statistics established by the method outlined by Imbrie are presented in Table 1. From these statistics, lines of the form $L = aB + b$ were formulated and are presented in Figure 5.

Where plotted, the lines of best fit were analysed to see if any significant difference in slope existed, using the formula

$$Z_1 = \frac{[a_1 - a_2]}{\sqrt{\sigma a_1^2 + \sigma a_2^2}}$$

where a_1 and a_2 represent the growth ratios of two lines being compared, and σa_1 and σa_2 are corresponding standard errors.

The results of these tests are illustrated in Table 2.

As all the calculated values of Z_1 are <1.96 , the indication is that there is no significant difference (at 99% level) in slope between the lines representing the "generic" groups.

As there is no significant difference between the slopes of lines of best fit, Imbrie outlines a further test, to test the hypothesis that the growth lines characterising the populations from which the two samples are drawn, are identical over the size ranges represented in the samples, by using the formula.

$$z_2 = \frac{B_0(a_1 - a_2) + (b_1 - b_2)}{\sqrt{\sigma a_1^2(B_0 - \bar{B}_1)^2 + \sigma a_2^2(B_0 - \bar{B}_2)^2}}$$

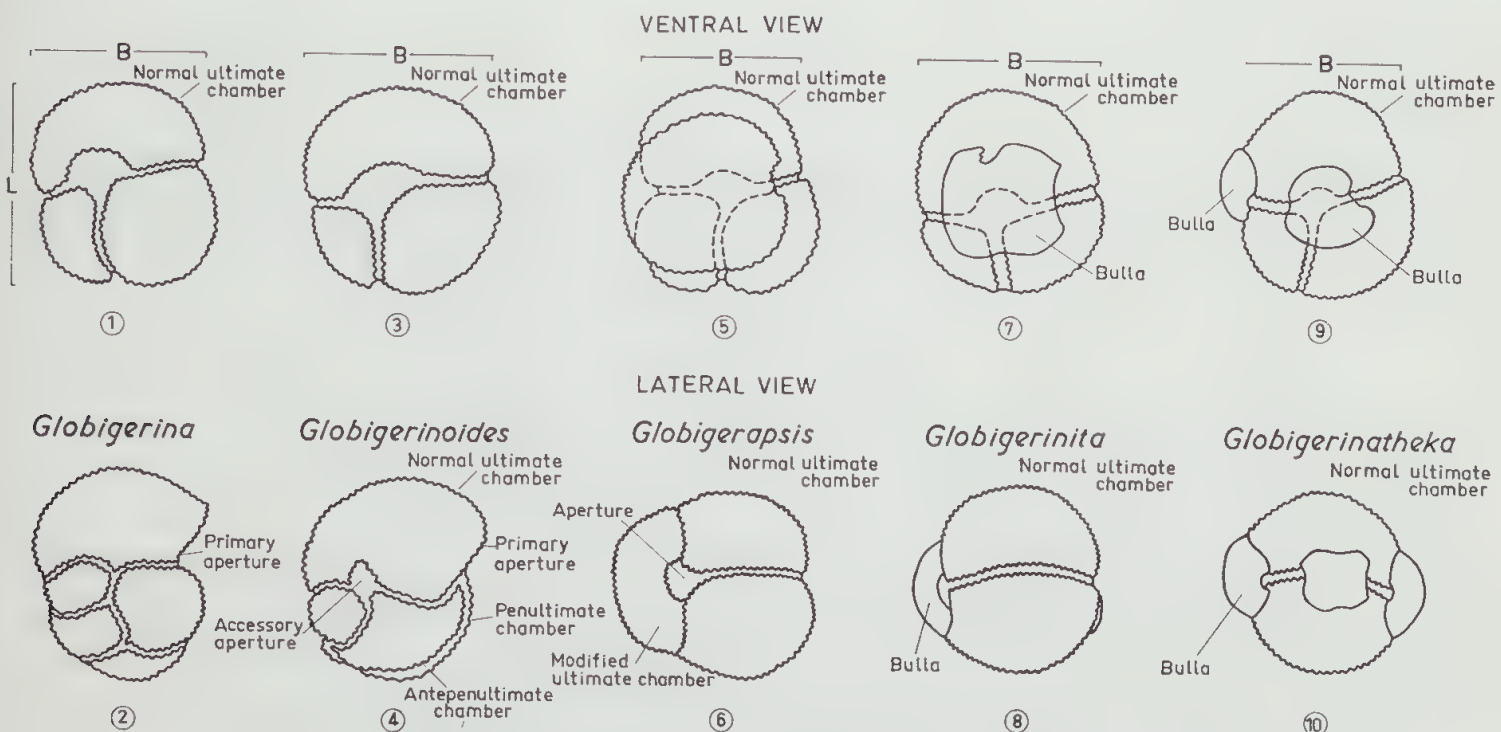


Figure 3.—Terminology used in discussing *Globigerapsis index* (Finlay).

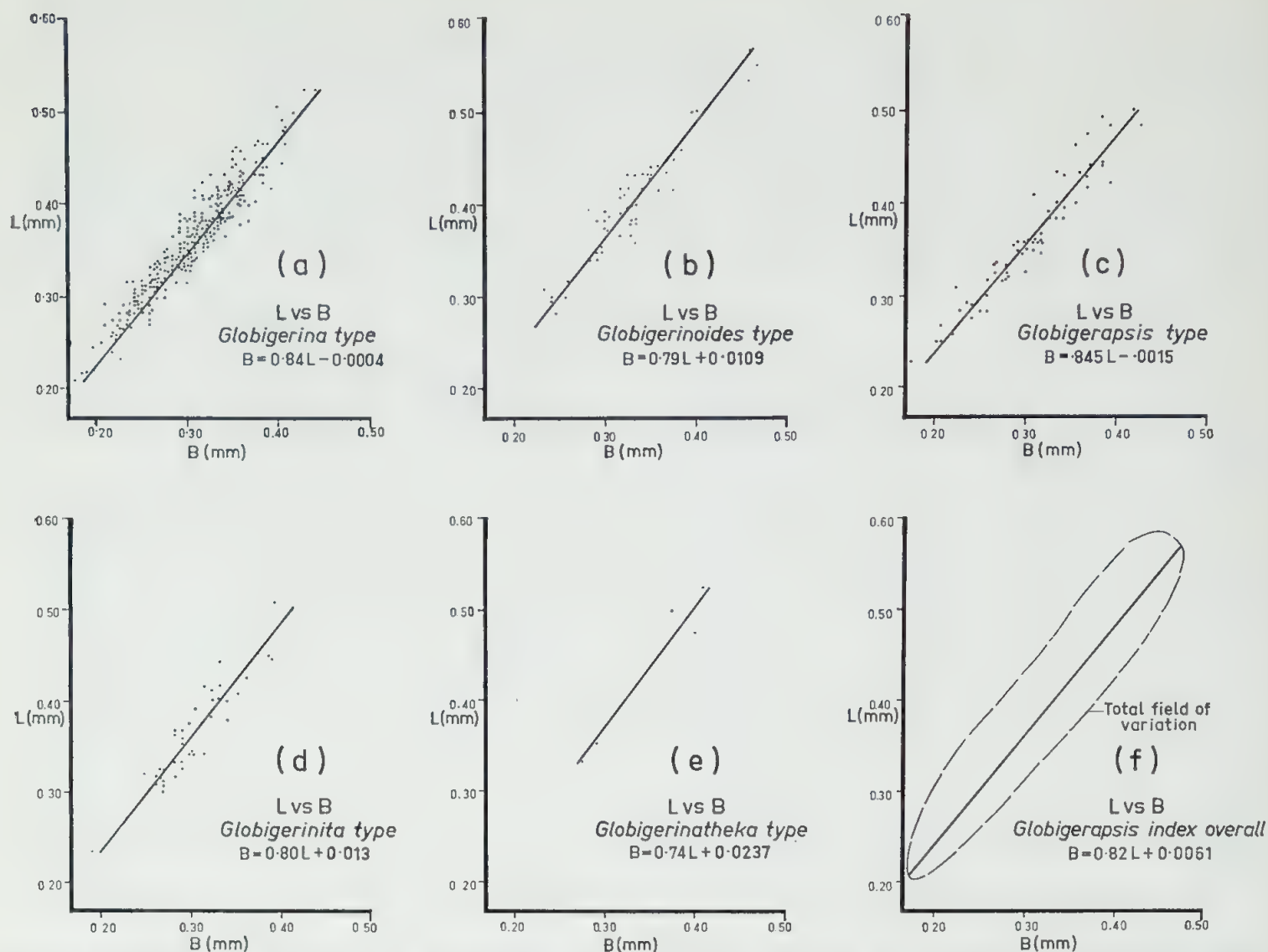


Figure 4.—Distribution of Length (L) and Breadth (B) for various "generic" groups within *Globigerapsis index* (Finlay).

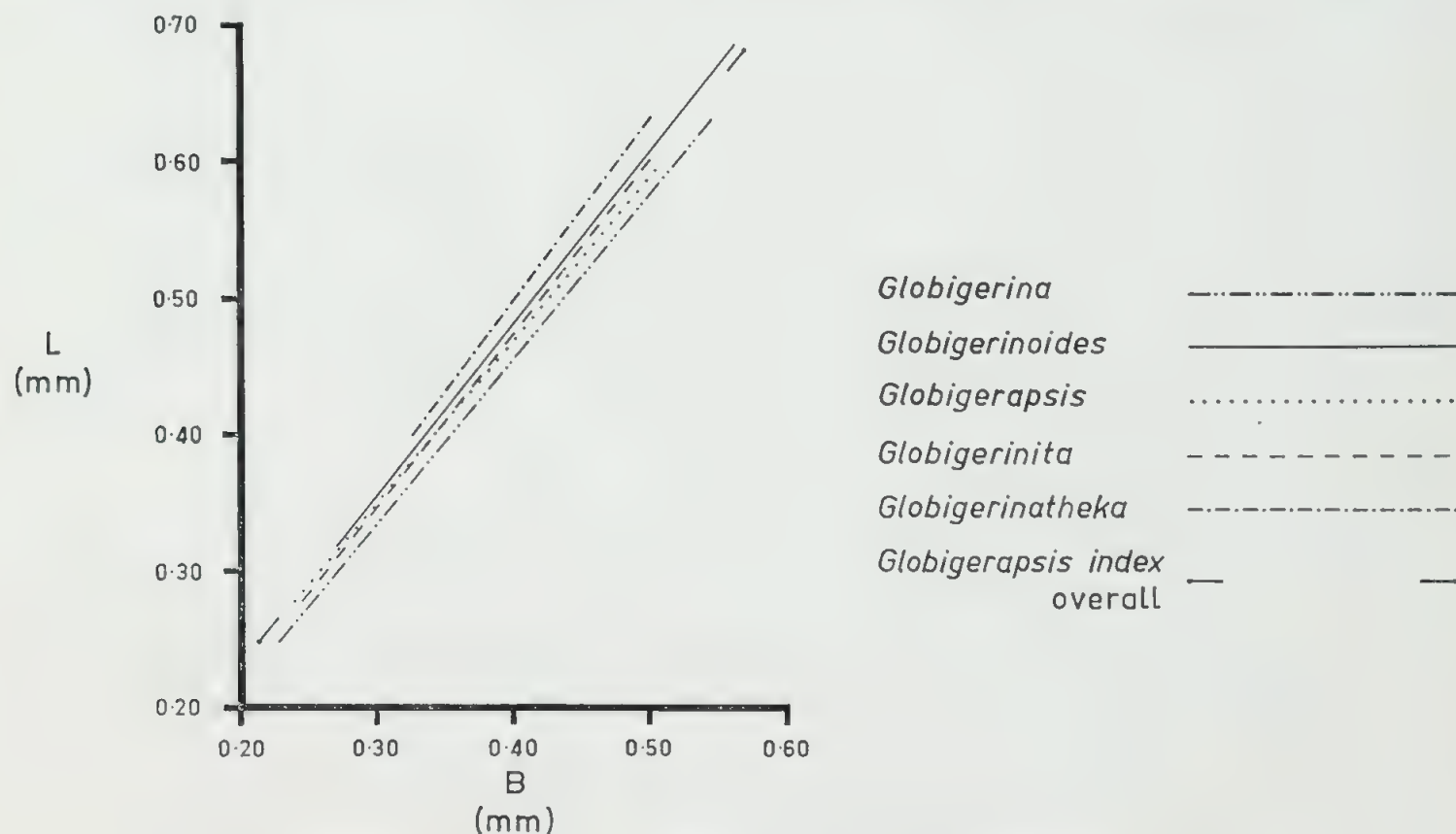


Figure 5.—Regression lines for various "generic" groups within *Globigerapsis index* (Finlay).

TABLE 1
Statistics calculated for the "generic" groups within *Globigerapsis* index (Finlay)

Statistic	<i>Globigerina</i>	<i>Globigerinoides</i>	<i>Globigerapsis</i>	<i>Globigerinita</i>	<i>Globigerinatheka</i>	Species Overall
N	271	54	63	42	6	436
Range of L	0.21-0.53mm	0.27-0.57mm	0.23-0.50mm	0.24-0.51mm	0.34-0.53mm	0.21-0.57mm
Range of B	0.18-0.45mm	0.24-0.47mm	0.18-0.43mm	0.19-0.42mm	0.26-0.41mm	0.18-0.47mm
\bar{L}	0.36mm	0.40mm	0.36mm	0.36mm	0.42mm	0.37mm
\bar{B}	0.31mm	0.33mm	0.31mm	0.30mm	0.34mm	0.31mm
S_L	0.06mm	0.063mm	0.068mm	0.055mm	0.090mm	0.063mm
S_B	0.05mm	0.050mm	0.057mm	0.044mm	0.067mm	0.051mm
a	0.843	0.790	0.845	0.801	0.742	0.820
b	-0.0004mm	+0.0109mm	-0.0015mm	+0.013mm	+0.0237mm	+0.0061mm
r	0.95	0.933	0.962	0.932	0.975	0.948
r_a	0.0001mm	0.0003mm	0.0002mm	0.0004mm	0.0006mm	0.0001mm
Equation of line	$B = 0.843L - 0.0004$	$B = 0.79L + 0.0109$	$B = 0.845L - 0.0015$	$B = 0.80L + 0.013$	$B = 0.742L + 0.0237$	$B = 0.82L + 0.0061$

TABLE 2
Results of significance tests on slope of lines. Figures presented are values of z_1 (see text)

	<i>Globigerina</i>	<i>Globigerinoides</i>	<i>Globigerapsis</i>	<i>Globigerinita</i>	<i>Globigerinatheka</i>	Species Overall
<i>Globigerina</i>	---	1.26	0.08	0.87	1.45	1.08
<i>Globigerinoides</i>	---	---	1.14	0.20	0.61	0.76
<i>Globigerapsis</i>	---	---	---	0.82	1.40	0.77
<i>Globigerinita</i>	---	---	---	---	0.73	0.41
<i>Globigerinatheka</i>	---	---	---	---	---	1.14

TABLE 3
Results of significance tests on position of lines with respect to L. Figures presented are values of z_2

	<i>Globigerina</i>	<i>Globigerinoides</i>	<i>Globigerapsis</i>	<i>Globigerinita</i>	<i>Globigerinatheka</i>	Species Overall
<i>Globigerina</i>	---	4.16	0.08	1.10	6.49	1.11
<i>Globigerinoides</i>	---	---	5.82	2.52	6.85	7.72
<i>Globigerapsis</i>	---	---	---	1.30	12.57	1.67
<i>Globigerinita</i>	---	---	---	---	6.61	0.32
<i>Globigerinatheka</i>	---	---	---	---	---	8.51

Taking the statistics shown in Table 3, those tests involving "*Globigerinatheka*" type individuals can probably be ignored as only six specimens were tested. Any other test values greater than 1.96 involve "*Globigerinoides*" type individuals. The discrepancy on the latter group can be explained conveniently, as it is often difficult to decide whether or not the ultimate chamber is, or is not, a little displaced from the normal growth spiral. When it is clearly displaced, the specimen is a "*Globigerapsis*" type; when it is not, it is a "*Globigerinoides*" type. There is a group in which it is hard to decide. When members of this group are included in "*Globigerinoides*", the measured length/breadth ratio is altered.

With these provisos in mind, it is clear that these "generically different" groups show no significant difference in spiral growth habit, and may be expected to be closely related. However, they also have in common, wall structure, sutural characters etc., and differ only in

characters relating to the ultimate chamber and its aperture(s) and bulla(e) i.e. they are similar in all characters generally accepted as being of specific importance. Thus it seems that these "generically different" groups are biologically conspecific.

The bulla

The bulla of *Globigerinita* and the modified ultimate chamber of *Globigerapsis* differ in wall structure as seen in thin section (see Table 4). The function of the bulla is debated. Hypotheses put forward for its use include:

- (1) It is a reproductive feature (Hofker, 1959; Pokorny, 1963),
- (2) It is a floating mechanism (Subbotina, 1953),
- (3) It is a "weight increasing" mechanism (Bolli, Loeblich and Tappan, 1957),
- (4) It is a floating and orienting mechanism.

TABLE 4
Measurements of wall characters of two specimens of Globigerapsis index (Finlay)

	<i>Globigerinita</i> type	<i>Globigerapsis</i> type
Wall Thickness—		
(a) bulla	10u	14u
(b) modified ultimate chamber		
Wall thickness of preceding chamber	22u	16–18u
Distance between pores—		
(a) bulla	6u	8–10u
(b) modified ultimate chamber		
Distance between pores in preceding chamber	11u	10u
Diameter of pores—		
(a) bulla	2u	3–4u
(b) modified ultimate chamber		
Diameter of pores in preceding chamber	3–4u	3–4u

Parker (1962, p. 246) states that a bulla is found in young and adult specimens alike and this seems a better reason against a reproductive function than the observations advanced by Hofker (1959) for a reproductive use. Assuming that she distinguishes young from adult specimens on the basis of size, Parker's observation may be put another way, i.e. that bullae are found not only on large specimens but also on smaller specimens. This may mean that mature specimens, small or large, carry bullae, rather than young and adult. The observations given on *Globigerina ampliapertura* (herein, *q.v.*) suggest that only part of the population carries bullae and that that part may be microspheric. This would support the contention that it has some sort of reproductive function.

To be a floating mechanism, the bulla would probably have to entrap gas. This solution is as likely as some others. Another possibility is that it also served as an orienting mechanism. The pores which are finer and more numerous on the bulla than on previous chambers would give rise to finer, more numerous and probably shorter, pseudopods than the normal chamber. This has been figured in a specimen of *Globigerinoides sacculifer* (Brady), (Kükenthal and Krumbach, 1921, p. 81, fig. 64). This imbalance of pseudopod concentration plus a possible gas concentration may favour a particular orientation of the test. Study of living globigerinids is necessary to clear up the question.

The ultimate chamber

Forms with more than one aperture in the ultimate chamber were found to be of three types.

(a) The "*Globigerinoides*" type in which the ultimate chamber is part of the normal growth spiral and possesses a primary umbilical aperture markedly larger than any supplementary apertures.

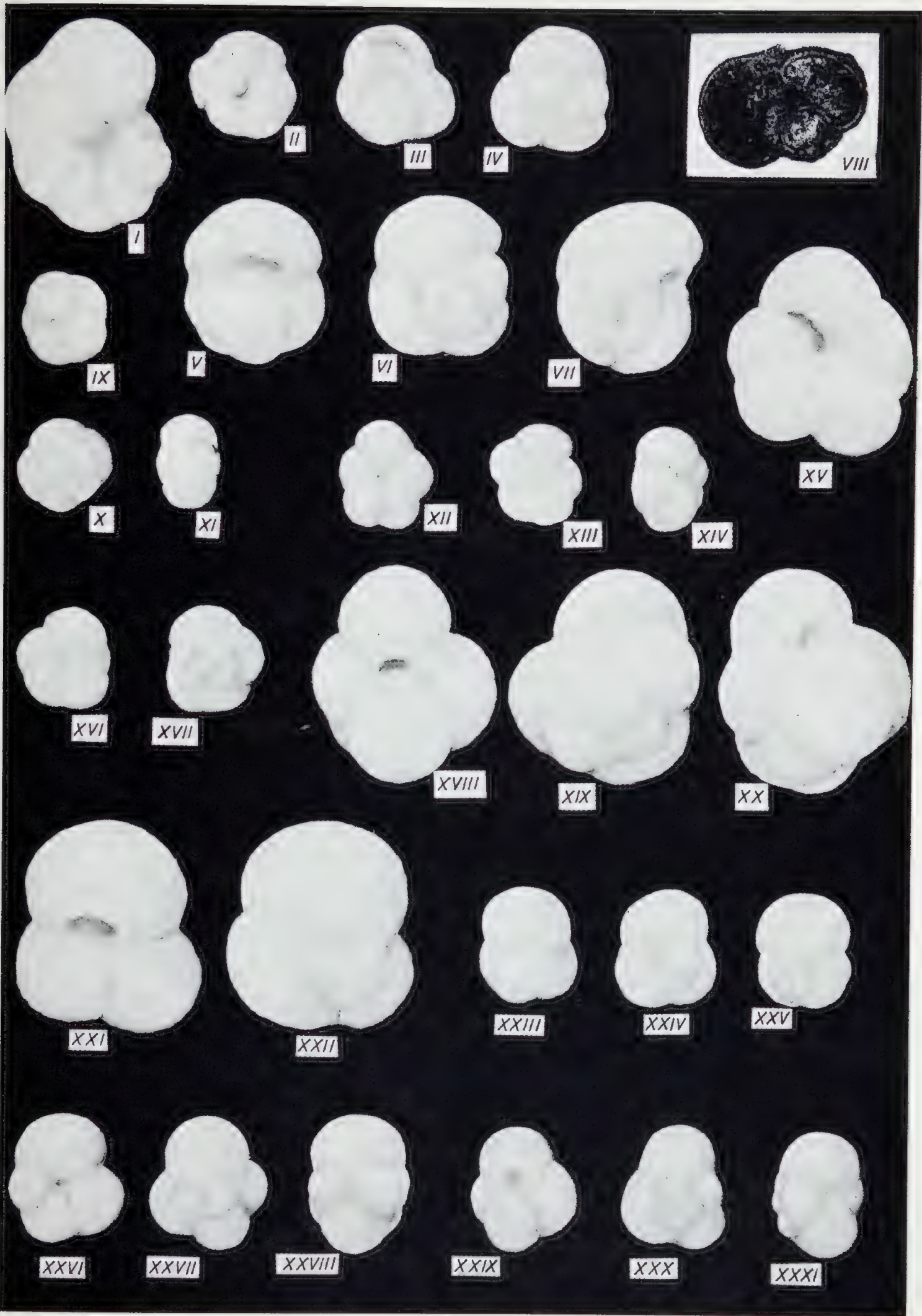
(b) The "*Globigerapsis*" type in which the ultimate chamber, although not part of the normal growth spiral, is texturally the same as preceding chambers, sits over the umbilicus of the

previously formed test and possesses more than one aperture of approximately equal size. The ultimate chamber is often hemispherical or rather flattened and reduced in size in contrast to the normal globular ultimate chamber. This "*Globigerapsis*" type ultimate chamber will be referred to throughout as a "modified ultimate chamber" to distinguish it from the bullae of the following types—the "*Globigerinita*" and "*Globigerinatheka*" types.

(c) The "*Globigerinita*" and "*Globigerinatheka*" types are characterised by the possession of bullae, the walls of which are texturally different from those of earlier chambers on the specimens on which the bullae are found. The walls are thinner, more finely perforate and the pores are closer together than in earlier chambers. The walls of the bullae and of the modified ultimate chamber of *Globigerapsis index* differ in thickness, pore size and pore density.

Figure 6 (facing page.)

- No. I, II *Globanomalina micra* (Cole); I. U.W.A.G.D. 59502, X135.
II. U.W.A.G.D. 59503, X70. Bullate specimen.
- III, IV *Globigerina cf africana* (Blow and Banner); U.W.A.G.D. 59505, X50.
- V–VIII *G. ampliapertura* form *ampliapertura* Bolli; V–VII U.W.A.G.D. 59506, X65. VIII Section of bullate specimen, U.W.A.G.D. 59536, X50.
- IX–XI *G. ciperoensis* form *angustiumbilitata* Bolli; U.W.A.G.D. 59507, X70.
- XII–XV *G. ciperoensis* form *basaapertura* n. form; Holotype, U.W.A.G.D. 59513; XII–XIV X70; XV. Enlarged view of apertural area, X135.
- XVI, XVII *G. cf echinata* (Bolli); U.W.A.G.D. 59508, X70.
- XVIII–XX *G. gortanii* form *praeturritilina* Blow and Banner; U.W.A.G.D. 59504, X120.
- XXI, XXII *G. jenkinsi* n. sp., Holotype, U.W.A.G.D. 59525, X135.
- XXIII–XXV *G. linaperta* form *linaperta* Finlay; U.W.A.G.D. 59509, X70.
- XXVI–XXVIII *G. martini* (Blow and Banner), U.W.A.G.D. 59510, X65.
- XXIX–XXXI *G. officinalis* subbotina, U.W.A.G.D. 59511, X65.



Conclusions

The statistical analysis presented here suggests fairly conclusively that all the specimens examined belong to a single population, and thus to a single species, even though some results of the z_2 test may be a little subjective. It also follows that they must all belong to the same genus.

It is proposed here that, ideally, genera must be defined in terms of (a) phylogeny, and (b) a set of morphological characters, and that species must depend on a population and not just on a single specimen. To date, the palaeontological habit seems to have depended on single specimens and a set of morphological characters.

Using the bases just proposed, *Globigerapsis* is here taken as a genus which developed in the Lower or Middle Eocene, probably from a *Globigerina* root stock, and which became extinct in the Upper Eocene, apparently without descendants. The characters of the ultimate chamber vary widely as indicated previously. It differs from *Globigerinoides* in that it belongs to a different lineage also derived from a *Globigerina* ancestral stock. Thus *Globigerapsis* is a valid genus and is here used to include that species defined by Finlay (1939B) as *Globigerinoides index*.

On the partly phyletic basis used here to define genera, such genera as *Catapsydrax*, *Tinophodella* and *Globigerinita* can only be used in the same sense as that in which *Globigerapsis* is here used, that is they must each belong to a different monophyletic group. *Tinophodella* and *Globigerinita* can probably be found in the one population and *Tinophodella* may well be a synonym of *Globigerinita* as has been suggested or implied several times already. *Globigerinita* should be reserved for nonhispid populations containing bullate forms as indicated by Parker (1962). These names cannot be used for individual specimens found in populations of species from a different lineage, and thus cannot be used for the specimens of *Globigerapsis* studied here.

Globigerinatheka, *Inordinatosphaera*, *Globigerinoita* and *Globigerinatella* are probably all only complex variants of populations belonging to species of previously defined genera and as such must be rejected.

Maximum diameter of figured specimens

- (a) *Globigerina* type 0.41mm
- (b) *Globigerinita* type 0.47mm
- (c) *Globigerinatheka* type 0.55mm
- (d) Section to show bulla structure 0.45mm.

Repository: (a) U.W.A.G.D.59532

(b) U.W.A.G.D.59533

(c) U.W.A.G.D.59534

(d) U.W.A.G.D.59535

Family GLOBOROTALIIDAE

Genus TURBOROTALIA Cushman and Bermudez, 1949

Turborotalia cf *centralis* (Cushman and Bermudez), 1937

Fig. 7, no. XLIX, L

cf *Globorotalia centralis* Cushman and Bermudez 1937, p. 26, pl. 2, figs. 62-65.

cf *Globorotalia* (*Turborotalia*) *centralis* Cushman and Bermudez; Cushman and Bermudez 1949, p. 42.
cf *Globorotalia centralis* Cushman and Bermudez; Bolli, Loeblich and Tappan, 1957, p. 41, pl. 10, figs. 4a-c.
cf *Turborotalia centralis* Cushman and Bermudez; Loeblich and Tappan 1964, p. C668, figs. 533, 6.
cf *Globorotalia centralis* Cushman and Bermudez; Jenkins 1965A, fig. 2.

Variation and Remarks

Eight specimens are questionably referred to this species. Maximum diameter varies from 0.20-0.42 mm with a mean value of 0.30 mm. Seven are sinistrally coiled.

The identification is very tentative as the diameters of the specimens in the present sample are very much smaller than is usual for *T. centralis*. Most recorded samples are quite large (0.4-0.7mm). The figures of the holotype (Cushman and Bermudez, 1937; Bolli, Loeblich and Tappan, 1957; Loeblich and Tappan, 1964) are of a specimen larger than, but otherwise extremely similar to the largest specimen found here and figured. The sample seems very different from figures of specimens other than holotype, for example that figured by Bolli (1957B, pl. 39, figs. 1-4).

On the basis of the rest of the planktonic foraminiferal fauna, the sediments are perhaps a little younger than those normally containing *T. centralis*. This also makes the identification a little questionable. Maximum diameter of figured specimen 0.42 mm.

Repository: U.W.A.G.D. 59537.

Turborotalia increbescens form *nana* (Bolli), 1957.

Fig. 7, no. LI, LII

Globorotalia opima nana Bolli 1957A, p. 118, pl. 28, figs. 3a-c.

Globorotalia opima nana Bolli; Blow and Banner (in Eames et al.) 1962, pp. 119-120, pl. 13, figs. Q-S.

? *Globorotalia opima* Bolli; Wade 1964, pl. 1, fig. 23.

Globorotalia nana Bolli; Jenkins 1965A, fig. 2.

Figure 7 (facing page.)

- | | |
|---------------|---|
| No. XXXII | <i>Globigerina ouachitaensis</i> form <i>ouachitaensis</i> Howe and Wallace; U.W.A.G.D. 59512, X60. |
| XXXIII, XXXIV | <i>G. praebulloides</i> form <i>praebulloides</i> Blow; U.W.A.G.D. 59519, X70. |
| XXXV, XXXVI | <i>G. senilis</i> Bandy; U.W.A.G.D. 59522, X55. |
| XXXVII-XXXIX | <i>G. tripartita</i> form <i>tapuriensis</i> Blow and Banner; U.W.A.G.D. 59523, X65. |
| XL, XLI | <i>G. yeguaensis</i> cf form <i>yeguaensis</i> Weinzierl and Applin; U.W.A.G.D. 59524, X55. |
| XLII-XLVIII | <i>Globigerapsis index</i> (Finlay); XLII-XLIV <i>Globigerina</i> type; U.W.A.G.D. 59532, X65. XLV <i>Globigerinita</i> type; U.W.A.G.D. 59533, X65. XLVI, XLVII <i>Globigerinatheka</i> type; U.W.A.G.D. 59534, X75. XLVIII Section through bulla and two chambers showing thin bulla wall, U.W.A.G.D. 59535, X45. |
| XLIX, L | <i>Turborotalia</i> cf <i>centralis</i> (Cushman and Bermudez); U.W.A.G.D. 59537, X65. |
| LI, LII | <i>T. increbescens</i> form <i>nana</i> (Bolli); U.W.A.G.D. 59538, X70. |
| LIII-LV | <i>T. permicra</i> (Blow and Banner); U.W.A.G.D. 59539, X70. |



XXXII



XXXIII



XXXIV



XXXV



XXXVI



XXXVII



XXXVIII



XXXIX



XL



XLI



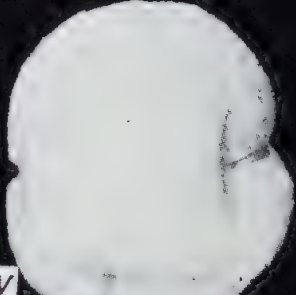
XLII



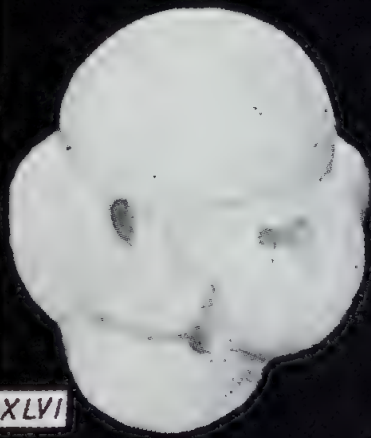
XLIII



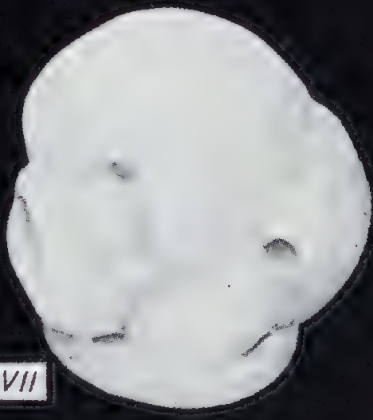
XLIV



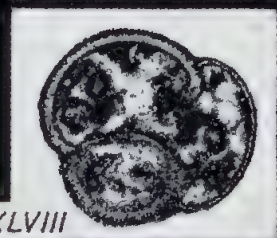
XLV



XLVI



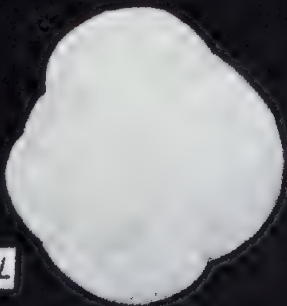
XLVII



XLVIII



XLIX



L



LI



LII



LIII



LIV



LV

Remarks

Of 37 specimens recovered, 35 are dextrally coiled. Maximum diameter range from 0.17 to 0.30 mm with an average value of 0.23 mm.

Although Blow and Banner (*in* Eames *et al.*, 1962, p. 118) compared and contrasted *T. increbescens* form *increbescens* with *T. centralis* Cushman and Bermudez, a better comparison seems to be with *T. increbescens* form *nana* (Bolli) (referred by them to *Globorotalia opima nana*). The only difference between the two forms is in the apertural characters. In this sample, similarities in size, granularity and perforation of the wall, rate of increase of chamber size etc., indicate that *T. opima nana* and *T. increbescens* (Bandy) are conspecific.

Blow and Banner noted that three 'subspecies', (the previously mentioned two, plus *T. i. opima*) are probably conspecific but did not give them the same specific name. The evolution of the species (*T. increbescens* and *T. opima*) as indicated by them—lineage A (p. 130-131)—is simplified if all forms are considered as one species.

The specific name *increbescens* has precedence over *opima* and the form name *increbescens* is added to distinguish the three forms of the species, i.e. *T. increbescens increbescens* Bandy, *T. increbescens opima* Bolli and *T. increbescens nana*. *T. opima* form *continua* Blow is separated as a species in its own right and becomes *T. continua*.

Maximum diameter of figured specimen 0.25 mm.

Repository: U.W.A.G.D. 59538.

Turborotalia permicra (Blow and Banner), 1962.

Fig. 7, no. LIII-LV

Globorotalia permicra Blow and Banner (*in* Eames *et al.*) 1962, p. 120, pl. 12, figs. N-P.

Remarks

This species is very similar to some figured specimens of *T. pseudobulloides* (Plummer). The only distinct morphological difference appears to exist in the apertural characters. Bolli (1957C, p. 73) stated that the aperture of *T. pseudobulloides* is a low arch whereas Blow and Banner (*in* Eames *et al.*, 1962, p. 120) stated that *T. permicra* has a high arch for an aperture. However this simple distinct difference is made less useful by Troelsen's (1957, p. 129) statement that the aperture of *T. pseudobulloides* is large, although his figures (Pl. 30, figs. 6-8) showed no significant size difference between the aperture of his specimens and those of Bolli (1957C, Pl. 17, figs. 19-21) and Loeblich and Tappan (1957, Pl. 40, figs. 3a-c; Pl. 41, figs. 1a-c; Pl. 42, figs. 3a-c; Pl. 43, figs. 3a-4c; Pl. 44, figs. 4a-6c; Pl. 45, figs. 1a-2c; Pl. 46, figs. 6 a-c), none of which shows the high arch possessed by *T. permicra*.

The maximum diameter of *T. pseudobulloides* ranges from 0.16 mm—0.50 mm (Bolli 1957; Troelsen 1957; and Loeblich and Tappan 1957) whereas that of the figured holotype of *T. permicra* is only 0.155 mm. There is probably some overlap but there may be a statistically significant difference in average values.

The most marked difference between the species is one of time range. *T. pseudobulloides* has an overall range of Lower and Middle Palaeocene while that of *T. permicra* seems to be upper Upper Eocene and at least Oligocene.

The rate of increase of chamber size is slightly less in the present sample than in the holotype.

Of 11 specimens in the sample, seven (64%) are sinistrally coiled. Average size is 0.23 mm with a size range of 0.17 to 0.27 mm—a value a little larger than that of the holotype.

Maximum diameter of figured specimen 0.25 mm.

Repository: U.W.A.G.D. 59539.

Correlation and age of the Nanarup Limestone Member

The nautiloids *Aturia clarkei* Teichert and *Teichertia prora* Glenister, Miller and Furnish (1956) suggest a Middle to Upper Eocene age for the Plantagenet Group, based on the faunas with which they are associated in northwest Western Australia.

If one accepts Bolli's (1957B) zonation of the Upper Eocene of Trinidad, the Nanarup planktonic fauna does not fit uniquely any one of his zones. However, if, following Bandy (1964), the *Globorotalia cerroazulensis* and *Globigerapsis seminvolutus* Zones are combined, the Nanarup fauna can be correlated with the combined zone.

There are marked discrepancies in the time ranges credited by different authorities to the various species found at Nanarup. One only has to compare the time ranges listed by Bolli (1957B), Blow and Banner (*in* Eames *et al.*, 1962), Jenkins (1965A) etc., to be forced to the conclusion that the same species may have markedly different time ranges in different parts of the world.

It seems that the Upper Eocene can be recognised internationally as only one zone on the basis of planktonic foraminifera, and that this international zone can be subdivided into two or three local subzones. The Nanarup fauna can be correlated directly and convincingly so far only with zonation schemes in Australia, New Zealand, Solomon Islands and Tanzania. This fact may be a reflection of an Upper Eocene planktonic foraminiferal faunal province.

In Australia, the fauna correlates with Carter's (1958 A and B) Faunal Unit 2 on the basis of present *Globigerapsis index*, *Globanomalina micra*, *Globigerina linaperta* and absent *Hantkenina*.

Ludbrook and Lindsay (1967) have proposed a zonation scheme very similar to that put forward by Jenkins (1965A) for New Zealand. In Ludbrook and Lindsay's terms, the fauna correlates with the *Globigerina linaperta* Zone. In Jenkins' scheme, correlation is with the Upper Runangan (upper part of *Globigerina linaperta* Zone and lower part of *G. brevis* Zone).

In Tanzania, Blow and Banner (*in* Eames *et al.*, 1962) recognised three zones in the Upper Eocene. The Nanarup fauna correlates well with the *Globigerina turritilina* (= *gortanii*) *turriti-*

lina Zone which is the uppermost of the three. Common species include *Globanomalina micra*, *Globigerina ampliapertura* form *ampliapertura*, *G. linaperta* form *linaperta*, *G. gortanii* form *turritilina*, *G. ciperensis* form *angustiumbilitata* etc. *Hantkenina* is absent from faunas in both areas.

McTavish (1966) gave a zonation scheme for the British Solomon Islands. The Nanarup fauna correlates with his *Globigerina ampliapertura*/*G. linaperta* Fauna.

By virtue of its position in the southern hemisphere zonation schemes, we know that the Nanarup fauna is very high in the Upper Eocene. In terms of the European subdivisions of the Upper Eocene, it probably belongs to the Wemmelian, Priabonian or Lower Ludian [in the sense in which those terms are used by Thenius (in Lotz, 1959)]. Following Gignoux (1955), the fauna is Ludian (= Wemmelian = Upper Priabonian).

Conditions of formation

If Loeblich and Tappan (1964, p. C116 *et seq.*) are correct in proposing that dominant dextral coiling in planktonic species is a record of warm water, the Nanarup fauna is a warm water one, as the fauna is about 95% dextrally coiled overall, with *Globigerina ampliapertura* form *ampliapertura* the only noteworthy exception. The diversity of the planktonic fauna also supports this contention. Many aspects of the benthonic fauna also support a warm water origin and these will be recorded elsewhere.

The planktonic element constitutes 10% of the foraminiferal fauna. This is consistent with a depth of formation of about 120 ± 60 feet (Phleger, 1960, p. 258, 259). Some aspects of the benthonic fauna suggest a little deeper formation but this also will be discussed elsewhere.

Acknowledgements

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9.—Sea Temperatures on the coast of South Western Australia

by E. P. Hodgkin* and B. F. Phillips*†

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Abstract

Surface water temperatures in Cockburn Sound, near Fremantle, are shown to follow the same seasonal cycle as air temperatures, but with a smaller range. The highest monthly mean temperature recorded was 24.7°C and the lowest was 12.8°C. Offshore water temperatures show a marked lag as compared with inshore temperatures and the annual range is smaller than either Cockburn Sound or near Fremantle. Water temperatures at Geraldton show the same pattern as in Cockburn Sound, but a slightly smaller range, and the mean is about 2°C higher.

Introduction

Ecological studies of marine animals are continually hampered by the lack of appropriate environmental data, normally available to workers in terrestrial situations. Of the measurable factors in the marine environment temperature is perhaps the most universally used. Its selection is, however, based not only upon ease of recording but upon established relationships between temperature and breeding, rate of growth, mortality and behaviour in many different species.

Sea water temperatures have been recorded by ships entering and leaving the Port of Fremantle for many years and have been taken by a number of special agencies, nevertheless they do not appear to have been collated and published in a form convenient to biologists. Charts published by the Royal Netherlands Meteorological Institute (1949), G.B. Meteorological Office (1949), and U.S. Navy, Hydrographic Office (1944) show ocean temperatures, month by month, as area means. Enormously valuable as these are, the very fact that they are mean values, and for the open ocean, limits their value to anyone interested in actual temperatures close to the coast.

Temperatures recorded

Since the establishment of the BP Oil refinery at Kwinana in Cockburn Sound, the maximum and minimum temperature of the cooling water has been taken daily at the intake. The daily mean temperatures have kindly been made available to us by the refinery management for the eight years 1960-67.

These temperatures then are those of surface water close to the shore in Cockburn Sound. They are summarised in Table 1. The 1960

and 1967 figures are shown in Figure 1, in which air temperatures recorded at the Perth Observatory during these years are also included.

Water temperatures at stations in Gage Roads and off Rottnest Island were recorded between 1949 and 1956 and these are published in the C.S.I.R.O., Division of Fisheries and Oceanography Station Lists Nos. 3, 14, 18, 24, 27 and 30. No recordings were made in these areas during the period 1960-67. The figures for 1953 are shown in Figure 2.

Surface water figures have been recorded weekly since 1966, in the harbour at Geraldton (at 1300 hours above a depth of 2 fathoms). The data for 1967 are presented in Figure 3.

Discussion

The following conclusions may be drawn from an examination of the data from Cockburn Sound (Table 1 and Figure 1).

(a) The annual curve of inshore water temperatures is very similar to that of air temperatures, with a peak in January or February and a minimum in July or August.

(b) As is to be expected, the range of water temperatures, 8.3 °C, is less than that of air temperatures 12.4°C (monthly mean water temperatures 1960-67, monthly mean air temperatures 1960 and 1967). Air temperatures averaged about 2°C higher for a short period in summer and 2°C lower for as much as six months in winter.

(c) Variation from one year to another is small.

(d) The highest monthly mean water temperature recorded was 24.7°C and the lowest was 14.5°C. Daily sea temperatures show a greater range; the highest temperature was 26.7°C and the lowest was 12.8°C. In every year figures of 25°C or over were recorded and usually occurred in three or four months each summer and in only one year did the figure not fall below 14°C. These then may be regarded as the biological maxima and minima.

(e) Because the figures show considerable consistency it is possible to use meteorological data to estimate water temperatures for periods when no recordings are available. This has proved useful in associating catch rates of juvenile crayfish with temperatures in areas for which no water temperature records were available.

From the water temperature recorded in Gage Roads and off Rottnest Island (Figure 2) the following points may be noted.

* Zoology Department, the University of Western Australia, Nedlands.

† Present Address: C.S.I.R.O., Division of Fisheries and Oceanography, Western Australian Marine Research Laboratory, Private Bag, P.O. North Beach, Western Australia, 6020.

TABLE 1
WATER TEMPERATURES IN COCKBURN SOUND IN THE FOREBAY AT BP's (KWINANA) REFINERY

*Monthly Means of Daily Maxima and Minima, and Maximum and Minimum
Temperatures in Degrees Centigrade*

Month	1960	1961	1962	1963	1964	1965	1966	1967	Mean
January	21.4 (20.5-25.6)	24.5 (21.1-25.6)	22.8 (21.1-25.0)	22.7 (20.6-25.6)	23.1 (20.6-25.0)	23.0 (20.6-25.6)	23.3 (21.1-25.6)	22.6 (21.1-25.0)	22.9
February	22.4 (21.6-26.1)	24.7 (22.2-26.1)	23.0 (21.1-25.7)	23.5 (20.0-25.0)	22.6 (19.4-24.4)	22.9 (20.6-25.0)	22.7 (21.1-25.0)	23.8 (22.2-26.1)	23.2
March	21.0 (20.5-25.0)	23.6 (21.6-26.1)	21.7 (20.6-23.9)	23.5 (21.1-26.7)	22.0 (18.3-25.0)	22.3 (20.0-25.0)	22.5 (20.6-24.4)	22.3 (20.0-25.0)	22.4
April	19.5 (18.9-23.9)	20.0 (19.4-22.8)	20.5 (18.9-22.2)	21.0 (17.8-23.9)	19.6 (17.8-21.7)	20.8 (19.4-23.3)	20.1 (17.8-22.8)	20.7 (18.3-23.3)	20.3
May	16.4 (16.1-21.1)	19.0 (17.8-21.1)	19.2 (16.7-21.1)	18.9 (16.7-21.1)	18.0 (15.0-20.0)	18.5 (16.7-21.1)	18.8 (16.7-20.0)	19.0 (16.7-21.7)	18.5
June	15.5 (15.0-18.3)	16.4 (13.9-17.8)	17.5 (16.1-18.9)	15.8 (14.4-17.8)	16.5 (15.0-18.3)	16.8 (14.4-18.3)	16.5 (13.9-18.3)	17.5 (16.1-18.9)	16.6
July	14.5 (13.9-16.7)	15.0 (13.9-16.7)	15.3 (13.9-17.8)	14.9 (13.3-16.1)	14.9 (13.9-16.1)	16.0 (14.4-18.3)	15.1 (13.9-16.7)	15.8 (13.9-17.8)	15.2
August	14.9 (14.4-17.2)	15.5 (13.3-17.2)	16.5 (15.0-17.8)	15.2 (13.3-17.8)	15.1 (12.8-16.1)	15.3 (14.4-17.2)	15.0 (13.3-16.7)	15.6 (14.4-17.8)	15.4
September	16.4 (15.0-20.0)	17.4 (15.0-18.3)	17.1 (15.6-20.0)	16.2 (15.0-17.8)	16.8 (14.4-19.4)	16.6 (14.4-18.3)	16.0 (15.0-17.2)	17.5 (15.6-20.0)	16.8
October	17.8 (15.0-21.1)	18.6 (16.1-21.1)	17.5 (15.0-20.0)	18.5 (16.7-21.1)	17.2 (15.6-20.0)	18.0 (15.6-20.0)	17.0 (13.9-18.9)	19.7 (17.2-22.2)	18.0
November	18.9 (16.6-22.2)	21.2 (18.3-23.9)	20.1 (17.2-23.9)	20.2 (18.3-23.3)	19.1 (15.6-21.7)	19.1 (16.7-22.2)	20.1 (17.2-23.3)	21.1 (18.3-23.3)	20.0
December	22.2 (18.9-25.0)	22.5 (20.0-25.0)	22.0 (18.3-24.4)	22.5 (20.0-25.0)	20.6 (17.8-22.8)	22.8 (20.6-25.6)	21.8 (19.4-23.9)	22.5 (20.0-24.4)	22.1

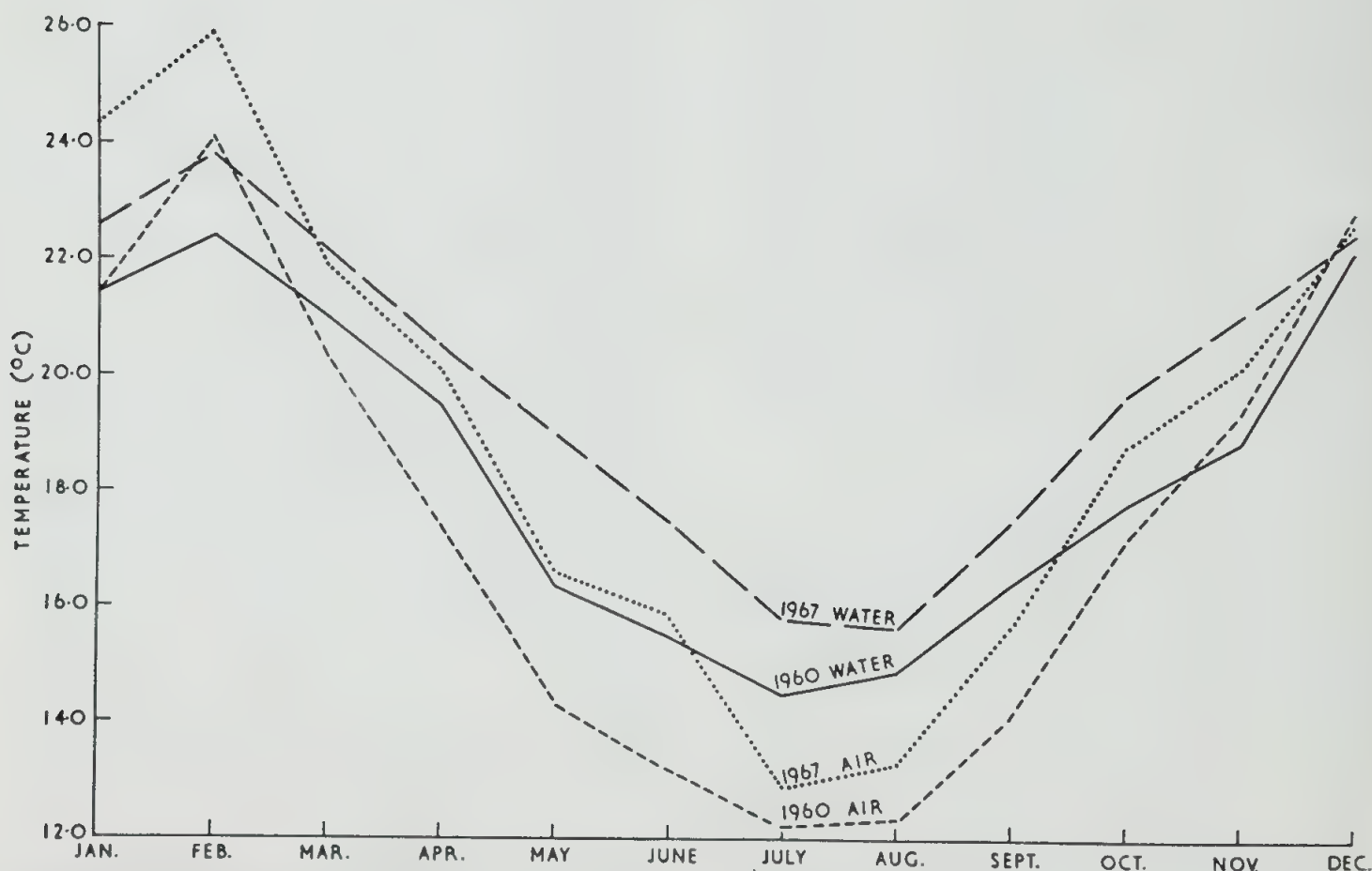


Figure 1.—Monthly mean surface water temperatures in the Forebay, BP's (Kwinana) refinery, Cockburn Sound, (mean of daily minimum and maximum) and monthly mean air temperature at Perth, Western Australia during 1960 and 1967.

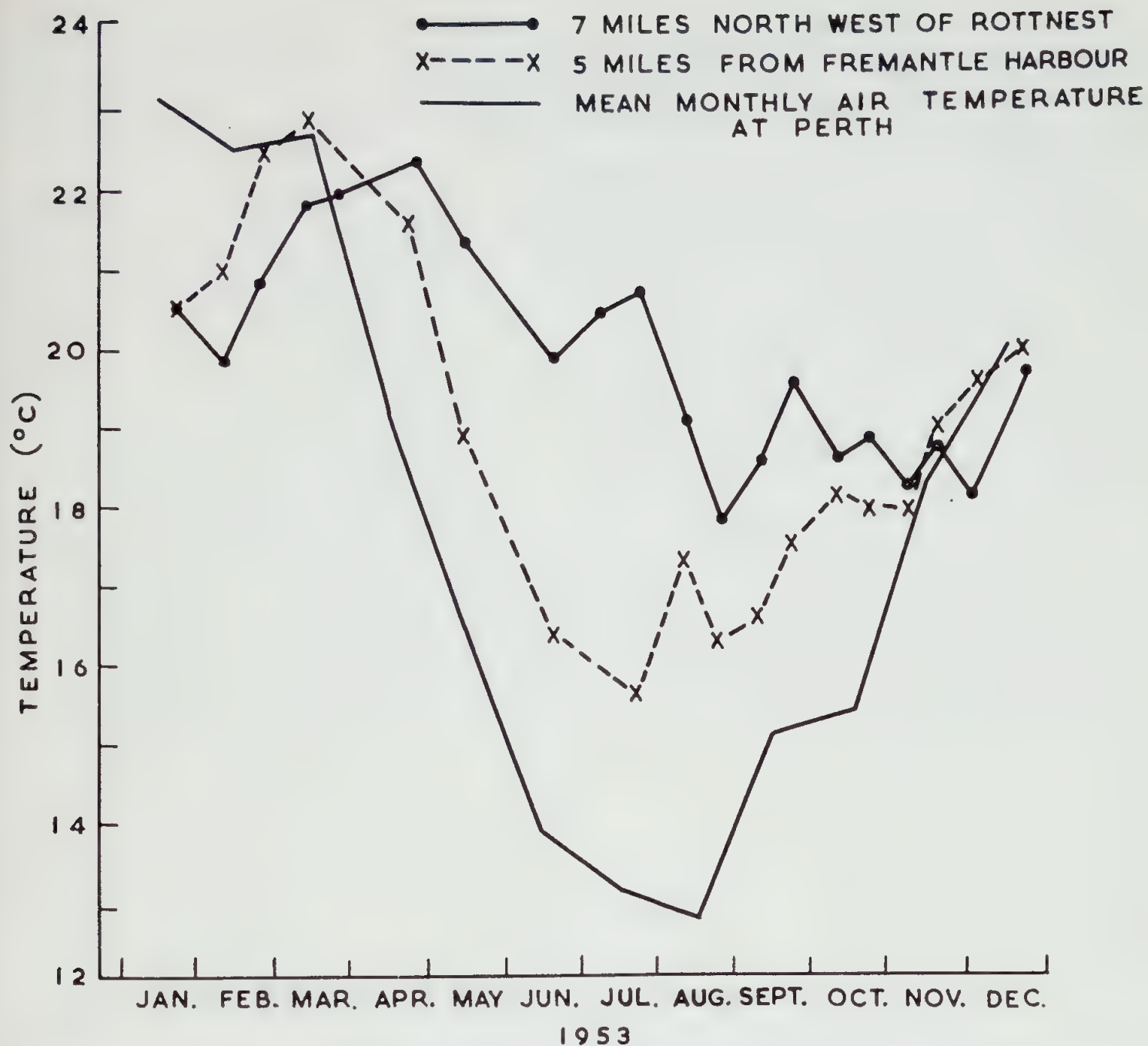


Figure 2.—Surface water temperatures from the "50 Metre Station" 7 miles north west of Bathurst Point, Rottneest Island, and Gage Roads, 5 miles from the entrance to Fremantle Harbour. Monthly mean air temperature at Perth, Western Australia, for the same period.

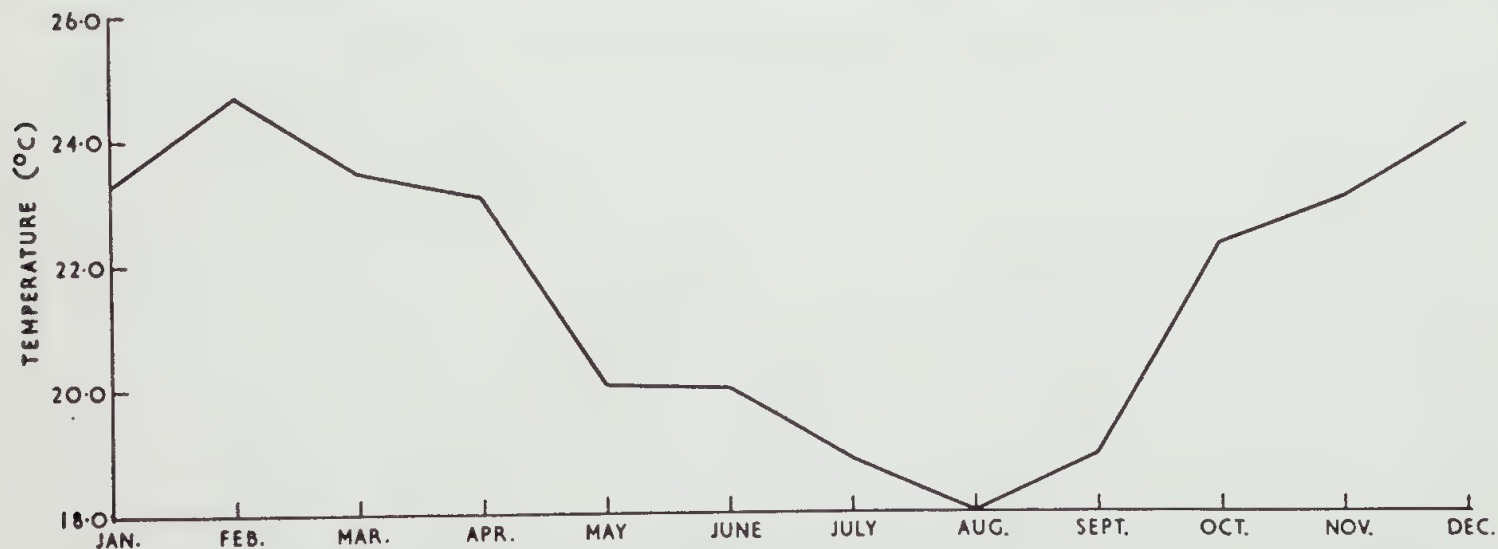


Figure 3.—Monthly mean surface water temperature at Geraldton, Western Australia, during 1967

(a) The curve from Gage Roads (5 miles west of Fremantle) is very similar to that for Cockburn Sound, though the summer peak tends to come later. The range of the monthly mean temperatures, 7°C is less than for Cockburn Sound.

(b) The figures for the station off Rottnest Island show an even smaller range, only 5°C and a more pronounced lag. The summer peak is sometimes not reached until May and the lowest winter figures also are considerably later than closer inshore. In 1952 the lowest figure was recorded in November.

It is not possible to draw reliable conclusions from the limited data recorded from Geraldton (Figure 3), however, the following points may be noted:

(a) The curve is similar to that recorded in Cockburn Sound and appears to follow the air temperature fairly closely, but with a smaller range.

(b) The observed temperature range is less than in Cockburn Sound, in any year.

(c) The mean is about 2°C higher than for Cockburn Sound or Gage Roads.

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